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The genetics of Neurospora—III.
Pure bred stocks and crossing-over in N. crassa

CARL C. LINDEGREN

(WITH PLATE 9 AND SIX TEXT FIGURES)

THE DEVELOPMENT OF PURE BRED STOCKS

The mode of segregation of the sex factors in the ascus of *Neurospora crassa* has been reported in a previous paper (Lindegren 1932b). This work involved a number of generations of inbreeding. The first generation consisted of the eight mycelia grown from the eight ascospores from a single ascus. The second generation was obtained by mating mycelia from two of these spores. The spores from seven asci of this generation were induced to germinate. All mycelia produced in the first two generations resembled the wild-type or *normal* mycelium.

The third generation was obtained by mating the mycelium from a first-generation ascospore with mycelia from second-generation ascospores. Mycelia were grown from 32 of these third-generation asci. Thirty-one of them produced ascospores from which only *normal* mycelia were grown. A single third-generation ascus produced four *normal* and four exceptional mycelia. These mycelia were *tan* as described below.

The sex factors in this exceptional ascus were segregated at the first division in the ascus. The factors for *tan* and *non-tan* were segregated at the second division (Lindegren 1932b, fig. 2, b). A mating was made between a *non-tan* and a *tan* mycelium from this ascus, and the ascospores from 55 asci were dissected and mycelia were grown from them. These mycelia fell into two classes, *tan* and *normal*, but there was a wide range of variation in each class. This shows that modifiers affect both the *tan* character and its *normal* allelomorph. In many asci, *tan* and *normal* were segregated at one division, and at least one modifier was segregated differently causing the two pairs of *normal* mycelia to be different and the two pairs of *tan* mycelia also to differ from each other. But members of each pair were always identical. This marked similarity of the two members of each pair is true of all the 55 asci in the f_1 generation.[1] It has also been found in all the many hundred asci from the spores of which the writer has grown mycelia. This proves that the third division in the ascus is equational. Of the 55 asci obtained from the f_1 generation, 48 contained

[1] I am using the symbol f_1 here to refer to the haploid vegetative mycelium developed from ascospores which are cut out after reduction. Strictly speaking, in case of these ascomycetes, the F_1 generation would consist merely of the diploid ascogenous hyphae and the young asci.

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four *tan* and four *normal* mycelia. It is possible that extreme modification of the *tan* gene prevented classification of the other seven asci. Both first- and second-division segregations of *tan* from its *normal* allelomorph were found to occur in the same perithecium.

Descriptions of the pure bred stocks

Black (B). On all media, the *black* mycelia produce a heavy growth of bright orange conidia. On concentrated corn-meal agar, the upper surface of the substrate becomes black. This does not occur on dilute corn-meal agar. *Black*, therefore, resembles the Mendelian character, abnormal abdomen (Morgan 1915), in being markedly dependent on both environment and genetic constitution. It is impossible to change a genetically *non-black* strain to *black* by transfer to richer medium.

Pale (P). Mycelia with the *pale* factor always produce lighter colored conidia than the *black* stock. The substrate in the *pale* cultures darkens on rich media, just as the substrate in the *black* cultures.

Even (E). The aerial hyphae form an even, velvety, orange growth.

Fluffy (F) and *albinistic* (A). These mycelia are very similar. The aerial growth is white, and no conidia, or only a very few, are produced. The *fluffy* mycelia produce numerous small sclerotioid bodies which are not so abundant in the *albinistic* mycelia.

Normal (n). *Normal* cultures resemble the wild-type fungus from which these stocks were developed. The inbred *normal* mycelia are extremely uniform. The f_1 generation *normal* (n) mycelia varied widely from each other.

Tan (T). These cultures are characterized by the development of a tan color in the substrate and few conidia.

Breeding experiments to build up pure bred stocks

A family tree (fig. 1) shows the various matings by which the pure bred stocks were built up. The numbers indicate the serial numbers of the respective asci. The arrangement of the ascospores in the ascus is shown by the four symbols, one for each pair of ascospores. In some cases asci were not dissected. This is indicated by "random." A dash indicates that the mycelium from neither one of the respective pair of ascospores was examined. Each horizontal line constitutes a sexual generation. The first ascus (114) is the progenitor for all the asci shown in the second row.

Black. This stock reproduced itself with perfect fidelity in every one of the seven generations.

Pale. A mating was made between two dark *normal* mycelia of the second generation. Two third-generation asci, resulting from this mating

were dissected. They contained two *normal*, two *tan*, and four *pale* ascospores. Sixty-five third-generation ascospores were selected at random.

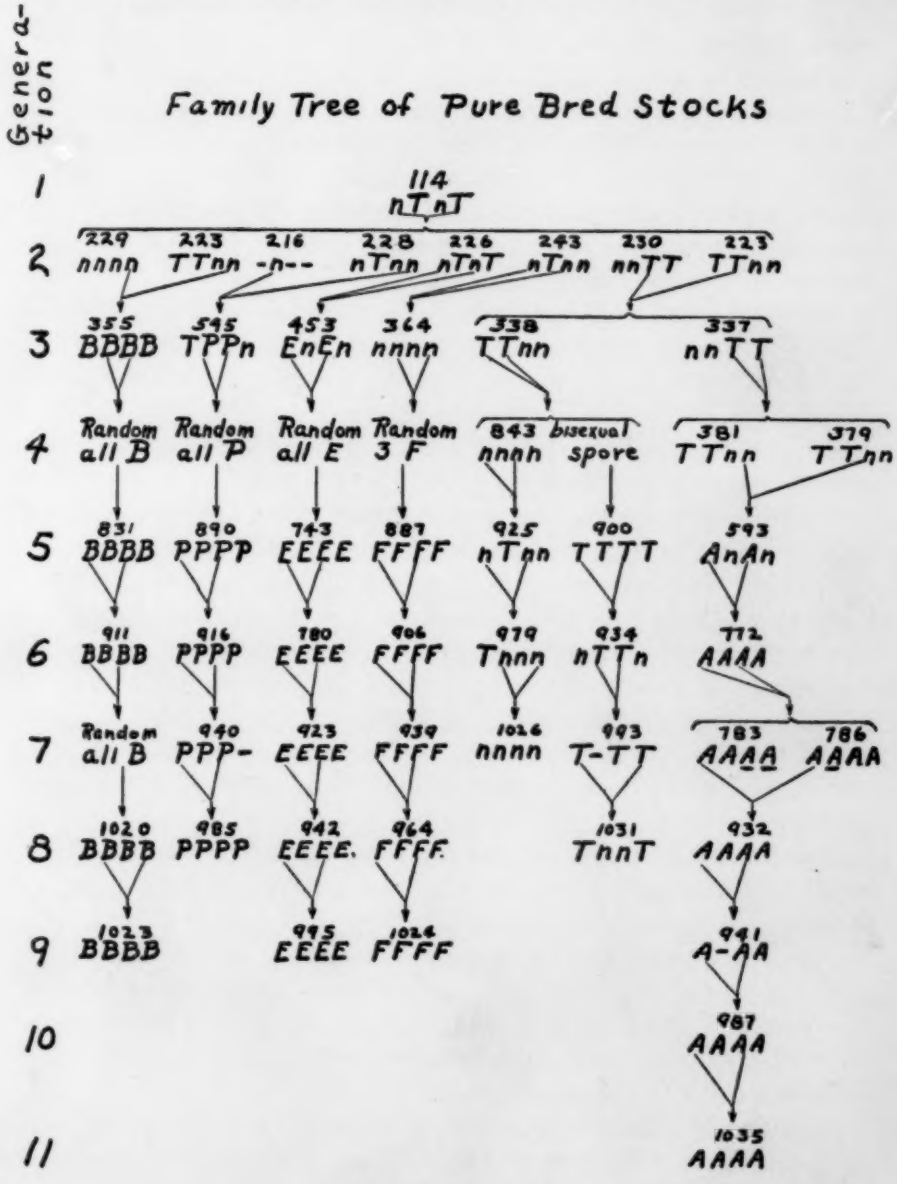

Fig. 1

The mycelia produced by them confirmed this ratio. Mating two of the *pale* mycelia produced only *pale* offspring for the next five generations.

Even. Two *normal* mycelia from ascus 226 were mated. Six of the asci that resulted from this mating were analyzed. They all contained four *even* and four *normal* ascospores. Two *even* mycelia from one of these asci were mated. Only *even* offspring were obtained for six succeeding generations.

Fluffy. Two *normal* ascospores from ascus 243 were mated. Fourteen third-generation asci, resulting from this mating, were analyzed. They produced only *normal* offspring. A mating was made between two mycelia from one of these asci. Thirty-seven ascospores were selected at random. Seventeen produced *pale*, 17 produced *normal*, and 3 produced *fluffy* mycelia, two of these *fluffy* mycelia were mated and only *fluffy* offspring were obtained in four succeeding generations.

The *black*, *pale*, *even*, and *fluffy* stocks all reproduced only their own types in succeeding generations. In this respect they differ markedly from the *tan* stock. On mating two *tan* mycelia, *normal* progeny were always obtained even after seven generations of inbreeding. In general, *tan* by *tan* matings produce half *tan* and half *normal* mycelia. Stocks of the *normal* mycelia produced from these *tan* parents have been built up. They reproduce their own kind in succeeding generations. It has not been possible to build up a pure bred stock of *tan* which produces only *tan* progeny.

Normal. An extensive series of experiments was performed in an attempt to produce a pure bred stock of *tan*. The results threw considerable light on the nature of the inheritance of the *tan* factor and its allelomorph. On mating two *tan* mycelia, *normal* progeny were produced. Although the *normal* and *black* cultures resemble each other closely, the substrate of the *normal* mycelia does not darken on any medium. A short sketch of the development of the *tan* and *normal* stocks will be given using the data in the family tree.

Tan mycelia from asci 230 and 223 were mated. Most of the asci dissected from this mating contained four *tan* and four *normal* ascospores. From ascus 338, two of the *tan* mycelia were again mated. In spite of the fact that both parents and grandparents were *tan*, some of the asci contained all *normal* ascospores. Two *normal* mycelia from one of these asci were mated. A fifth generation was produced, from which three asci were dissected. One ascus contained only *normal* ascospores. Two asci contained six *normal* and two *tan* ascospores.

A mating was made between two of the *normal* mycelia from this fifth generation (ascus 925). Four asci were dissected. Two asci contained only *normal* ascospores. Two asci contained two *tan* and six *normal* ascospores. Two of these *normal* ascospores were mated. Five asci dissected from this mating produced only *normal* mycelia.

Tan. One of the asci produced by mating the two *tan* mycelia from as-

TABLE 1

Description of asci analyzed in the inbreeding of the black, pale, even, and fluffy stocks

GENERATION	BLACK			PALE			EVEN			FLUFFY		
	NO. ANALYZED ASCI	SPORES	CHARACTER	NO. ANALYZED ASCI	SPORES	CHARACTER	NO. ANALYZED ASCI	SPORES	CHARACTER	NO. ANALYZED ASCI	SPORES	CHARACTER
3	18		BBBB	2	65	TPPn 17T:17n: 31P	6		EnEn	14		nnnn
4		15	all B		25	all P		150	all E		37	17n:17P: Clon 3F
5	4	15	BBBB all B	2		PPPP	3		EEEE	10		FFFF
6	5		BBBB	4		PPPP	4		EEEE	6		FFFF
7		10	all B	2		PPP–	3		EEEE	1		FFFF
8	4		BBBB	6		PPPP	2		EEEE	5		FFFF
9	3		BBBB				4		EEEE	2		FFFF

cus 338 contained four bisexual ascospores. This is the only case in which any bisexual ascospores have been found in *N. crassa*. The perithecia from each of these bisexual ascospores all contained only the ordinary eight-spored *N. crassa* asci. Most of these asci contained four *tan* and four *normal* ascospores. But one of the asci contained only *tan* ascospores. Two of the *tan* mycelia, from this ascus, were mated. Two of the asci thus produced were dissected. They both contained four *tan* and four *normal* ascospores.

Two of the *tan* mycelia from ascus 934 were mated. Four asci were dissected. These asci had been mutilated so that no more than six ascospores were obtained from a single ascus. Two asci contained both *normal* and *tan* ascospores. In one ascus, 993, all six ascospores were *tan*. Two of these were mated. Four asci were obtained. Each contained four *tan* and four *normal* ascospores.

Albinistic. The *albinistic* stock was developed in the course of an attempt to produce a pure bred stock of *tan*. *Tan* mycelia from asci 223 and 230 were mated. The asci from this mating contained both *tan* and *normal* ascospores. Two of the *tan* mycelia from ascus 337 were mated. Again the progeny were half *tan* and half *normal*. Some of the *normal* mycelia showed a marked tendency to produce non-conidial hyphae. A mating was made between two such *normal*-like mycelia. The asci resulting from this mating contained four *albinistic* and four *normal* ascospores. But there was a third character involved. Some of the *albinistic* cultures had *tan* substrates and reduced aerial mycelium. Some of the *normal* cultures were *tan*. The italic letters *A* and *n* are used for mycelia showing the tan character. Table 3 shows that seven of the asci contained four *normal* and four *albinistic* ascospores, with no evidence of the *tan* character. Thirteen of the asci contained either *A* or *n* types of ascospores. One of the asci contained eight *normal* ascospores.

An ascus that did not contain either an *A* or an *n* ascospore was selected. Two of the *non-tan albinistic* mycelia from this ascus were mated. Table 2 shows that the eight asci examined contained only *albinistic* ascospores. But some of these *albinistic* mycelia developed tan substrates (*A*).

Again, one of the asci which did not contain *tan* ascospores was selected. A mating was made between two of the *albinistic* mycelia from this ascus (772). Six asci from this mating were examined. All produced *albinistic* mycelia. Three asci produced no *tan* ascospores. One ascus produced two *tan* and six *non-tan* ascospores. Two produced four *tan* and four *non-tan* mycelia.

For the eighth generation, *albinistic non-tan* mycelia were selected from asci which had also produced *albinistic tan* mycelia. These *non-tan albinistic* mycelia were mated, and five of the resulting asci examined. All con-

tained *non-tan albinistic* ascospores. It was concluded that the stock was now free from the *tan* factor. Three more generations were cultured and no more *tan* mycelia were produced.

The failure to produce a pure bred stock of *tan* was not due to failure to establish a uniform environment. When the other pure bred stocks are reproduced vegetatively, the transplants are invariably exactly like the parent cultures. This is not true of the inbred *tan* stock. The first culture

TABLE 2

Description of the asci analyzed in the inbreeding of the albinistic stock

GENERATION	ANALYZED	CHARACTER
Fifth	21 asci	7 AAnn 6 AAn*n*[a] 4 A*A*nn 2 *AA*nn 1 AA*n*n 1 nnnn
Sixth	8 asci	4 AAAA 3 AAA*A* 1 AA*AA*
Seventh	6 asci	3 AAAA 1 AAA*A* 2 AA*AA*
Eighth	5 asci	5 AAAA
Ninth	1 ascus	1 A—AA
Tenth	1 ascus	1 AAAA
Eleventh	4 asci	4 AAAA

[a] An italized letter indicates that the particular pair of ascospores showed the *tan* character in addition to the one indicated by the symbol.

made by a polysporous transfer from a *tan* culture usually does not have a *tan* color in the substrate, and produces an abundance of conidia. That is to say, it resembles *normal* very closely. When vegetative transfers are made by means of single conidium cultures, *tan*, *normal*, and intermediate cultures are obtained. *Normal* stocks can be obtained in this manner which do not revert to *tan* again following either polysporous or monosporous transfers. This is an irreversible variation. However, it has not been possible to build up stocks of *tan* by monosporous transfers which did not revert to *normal* on subsequent monosporous or polysporous transfer. This

indicates that the *tan* mycelia are heterokaryotic, containing both *tan* and *normal* nuclei. This heterokaryosis probably arises as the result of a mutation of the gene at the *tan* locus to the *non-tan* allelomorph.

Another example of a variation due to heterokaryosis is the following: One of the two unisexual component clones of a race of *Neurospora tetrasperma* produced only a few conidia and darkened the substrate. The other produced an abundance of conidia and did not darken the substrate. The bisexual thallus contained nuclei of both sexes in a common cytoplasm. It was intermediate in appearance and produced perithecia. Such a bisexual thallus was treated by X-rays and subcultured. All subcultures were of the type with a black substrate and few conidia. They were unisexual. A sufficient number of subcultures was made to indicate rather strongly that the other sex had not survived the treatment with X-rays. Without knowledge of the heterokaryotic constitution of such a bisexual thallus (Dodge 1928), and the nature of the cultural characters of the different sexes, it would have appeared that a mutation had been produced by X-radiation. This variation is not the result of mutation, but of the destruction of one type of nucleus in a heterokaryotic mycelium. It is possible that some of the opinions that have been advanced as to the extreme mutability of fungus genes have arisen from experiments with such heterokaryotic stocks which are readily susceptible to variations in the medium.

In the course of the development of most of these stocks, there has occurred the sudden appearance of a new character following inbreeding. The sudden reduction of variability which has accompanied the continued inbreeding in the case of the *black*, *pale*, *even*, *fluffy*, and *albinistic* stocks, indicates that they were produced by the segregation of preexisting genes into separate lines, rather than by new mutations. The variability of the *normal* mycelia in the second generation has been described. Inbreeding these various *normal* (?) mycelia resulted in the appearance of *black*, *pale*, and *even* mycelia in the third generation. *Black* resembles the dark *normal* cultures of the second generation so closely that it is difficult to call it a new form. *Pale* also resembles the dark *normal* of the second generation. *Even*, however, is decidedly different from any mycelia found in the second generation. It is an entirely new type. But the *normal* (?) mycelia from ascus 226 differed from the other second-generation *normal* mycelia in producing bright orange substrates. The production of *even* and *normal* ascospores by mating two of these mycelia with orange substrates, and the stability of the line from this point on, indicate the segregation of a gene, which modifies *even* to *normal*, from the *even* gene.

Fluffy cultures did not appear until the fourth generation, and, again, as stable segregates after inbreeding two generations of apparently *normal*

parents. This may also indicate that a gene modifying *fluffy* toward *normal* had been segregated from *fluffy*.

Albinistic cultures did not appear until the fifth inbred generation, although the fourth-generation *normal* (?) parents of this stock gave evidence of the presence of the *albinistic* gene. Again, this is an indication of the segregation of modifiers of *albinistic* toward *normal* from the *albinistic* gene, rather than a spontaneous mutation.

The fact that continued inbreeding of the unstable *tan* stock always produces some *normal* mycelia indicates that the *tan* gene mutates with rather high frequency to *normal* or *non-tan*. The resulting *normal* mycelia are stable and very seldom revert to *tan*. Genes modifying *tan* to *normal*, which have been shown to exist, may explain the fact that *normal* by *normal* matings occasionally produced *tan* mycelia. Such modifiers may account for the second-generation asci containing two *tan* and six *normal* and some of those containing eight *normal* ascospores. However, since the *tan* and *non-tan* genes were apparently segregated from each other in asci 381 and 379, the reappearance of *tan* in the progeny of the *normal* mycelia from these asci may be the result of a new mutation of the *normal* allelomorph to *tan*. The original appearance of *tan* in ascus 114 and again in the inbred *albinistic* line gives a total of two mutations from *normal* to *tan*. (However, both of these mutations may not have involved the same locus.) The reverse mutation of *tan* to *normal* occurs with high frequency as is shown by the fact that inbreeding of *tan* for eight generations still produces stable *normal* mycelia. We can conclude that the characteristics of the *black*, *pale*, *even*, *fluffy*, and *albinistic* stock are determined by stable genes, while the characteristics of the *tan* stock are determined by an unstable gene which mutates rapidly to *normal*. However, it is indicated that the *tan* mutation probably involves only a single locus and it therefore follows that the genes in all the other loci of the *tan* stock are stable.

In most studies of variation in fungi, the so-called "mutations" have occurred in clones, and the mycelia were propagated as clones. The variants were often obtained following treatment with poisons or heat. Although this type of treatment is not highly effective in producing point mutations in good genetic material, it is most effective in producing "Dauermodifikationen." It might also destroy or favor one type of nucleus in a heterokaryon. Barnes (1929) described some interesting variations in *Eurotium herbariorum*. These variations were induced by heat-treatment. Strict clonal propagation was not practised. Polysporous transfer of ascospores (sexual spores) and conidia (asexual spores) were made. It was these mixed inocula which were subjected to heat-treatment. The variants differed markedly in their stability. Many tended to revert to normal.

Barnes' data show that the most variable forms produced perithecia and ascospores. But the stable ones did not. He did not call attention to this relation. It seems probable that "Dauermodifikation" and the segregation of mutant types by sexual reproduction were involved in the production of the variants. It would be interesting to know if the ascospores were more resistant to the heat-treatment than the conidia.

Miss Heldmaier (1930) carried on a series of experiments on the effect of changes of environment on the ability of various strains of *Schizophyllum* to form clamp connections. This fungus has the tetrapolar type of sex. An AB strain could be altered so that it could copulate with an aB strain. This was assumed to mean that the AB strain was changed, by "modification" of the B gene, to an Ab strain. But another interpretation may seem more probable since it was not proved that a change had been produced in a "factor," only that its expression had been changed.

The facts that it is possible to establish true breeding forms of *Neurospora crassa* by continued inbreeding, and that both members of each of the four pairs of ascospores are identical (no matter how great the variability of the progeny of a mating may be) are strong arguments for believing that most of the genes of this fungus are stable genes.

CROSSING-OVER IN NEUROSPORA CRASSA

The *pale* race is also genetically *tan*, really the double mutant type *tan pale*, but the character *tan* is masked by the *pale* character. That is, *tan pale* mycelia can not be distinguished by inspection from the simple *non-tan pale* strain which may be obtained by segregation in F_1 from a cross of this double type with the *normal* race. *Fluffy* produces practically no conidia. The aerial mycelium is white in color and fluffy in texture. The substrate is colorless, that is, *non-tan*, and genetic tests have shown that this strain does not carry *tan*. Reciprocal matings of these two races were made, and more than 90 percent of the 880 haploid ascospores, produced in 110 asci, were grown and classified for mycelium characters, and a member of each pair of ascospores was tested for sex. The progeny (disregarding *tan* and sex) fell into the following four classes: *pale*, *fluffy*, *pale fluffy* and *normal*. The production of the wild-type class is proof of the fact that each stable haploid race carries the normal allelomorph of the gene which gives the other its characteristic difference from wild-type. In other words, the *pale* race carries the *non-fluffy* gene, and the *fluffy* race carries the *non-pale* gene. The two mutations are not multiple allelomorphs due to mutations in the same locus, but are due to mutation in two separate loci. Since these races are distinguished by characteristics of haploid mycelia developed from individual ascospores, there is no question of or confusion through

dominance and recessiveness, such as is met with in studies of diploid organisms. Each mutant gene is designated by a symbol which is a capital letter and its normal allelomorph is represented by the corresponding small letter. Therefore, the formula of the haploid *pale* parent is Pf, and the formula of the haploid *fluffy* parent is pF. The zygote (ascus nucleus) formed by mating these two races would contain two genes corresponding to each locus. It would be heterozygous for both *pale* and *fluffy*. Its formula would by P/p, F/f (or P f/p F, if the two are in the same chromosome). Reassortment of these genes in meiosis to form haploid ascospores (containing one gene from each pair) would result in the following classes:

P f *pale non-fluffy*, p F *non-pale fluffy*, P F *pale fluffy*, p f *non-pale non-fluffy*.

The first division of table 3 shows the frequency of these four types of ascospores among the 440 pairs of ascospores dissected from the 110 asci of the above cross. It has already been shown (Lindegren 1932b) that only the first two divisions in the ascus are reductional. The third division is

TABLE 3

Combinations in 440 pairs of ascospores, summarized for pale and fluffy, fluffy and sex, pale and sex

COMBINATIONS	TYPE	NO.	%	TYPE	NO.	%	TYPE	NO.	%
Original	Pf	114	51.8	F−	111	51.0	P+	169	77.5
	pF	114		f+	111		p−	169	
New	PF	106	48.2	F+	107	49.0	P−	49	22.5
	pf	106		f−	107		p+	49	

equational[2] (mitotic) for all genes. The two members of each pair of ascospores (1 and 2, 3 and 4, 5 and 6, 7 and 8) are identical genetically. This gives a maximum of four genotypes for the eight ascospores from any one ascus. This shows that *Neurospora crassa* and *Ascobolus magnificus* have different nuclear mechanisms, and indicates strongly that the zygote nucleus in *Neurospora crassa* is diploid. Proof of the diploidy of the ascus nucleus is as follows: All asci examined contained four *pale* and four *non-pale* ascospores, as well as four *fluffy* and four *non-fluffy* ascospores. Therefore, the ratio of *pale* to *non-pale* and *fluffy* to *non-fluffy* in the total population was 1:1. If the ascus nucleus were tetraploid in *Neurospora crassa*, this ratio could not be obtained without a second meiosis. In the absence of brachymeiosis, a ratio of 1:4:1 would be found (Haldane 1930) in the total population (not from each ascus). The diploid genotypes of this ratio

[2] Since this division is invariably equational it cannot be a brachymeiosis (Gwynne-Vaughan and Williamson, 1932) in the case of *N. crassa*.

would be, 1 *pale pale:* 4 *pale non-pale:* 1 *non-pale non-pale*, and the same in the case of *fluffy*. This, therefore, is the condition which would obtain if the ascus nucleus were tetraploid and a brachymeiosis did not occur. Since this ratio is not found and brachymeiosis does not exist in *N. crassa*, the other alternative is that the first fusion, said by some to occur at the origin of the perithecium, is followed by a reduction in the crozier or previously. In such a case the two haploid nuclei fusing in the young ascus should be both *pale* in 25 percent of the cases and both *non-pale* in 25 percent of the cases, while only 50 percent of the young asci would be heterozygous for *pale* and *non-pale*. The same reasoning applies in the case of *fluffy* and *non-fluffy*. Since every ascus nucleus was heterozygous for both of these pairs of genes, a perithecial fusion, if such there be, is not followed by a reduction before the formation of the crozier. Therefore, only a single fusion occurs in *N. crassa* and the ascus nucleus is diploid. This diploid nucleus is immediately reduced in the normal way by a meiosis involving only two reduction divisions.

Since the diploid zygote nucleus in the above cross was heterozygous for still another pair of genes, $+-$, the number of possible classes of ascospores was eight, as follows: Pf+, Pf−, pF+, pF−, PF+, PF−, pf+, and pf−. In the absence of linkage, each of these eight classes should occur in equal numbers in random samples of ascospores. But any one ascus would contain a maximum of four of these types of ascospores, and some would contain only two types.

In the absence of linkage, the four possible classes with respect to *pale* and *fluffy* should occur in statistically equal numbers, and the data show that equality is approximated. The practical equality of the original combination with the recombination classes shows that these two genes are not linked. When four Pf ascospores are present in one ascus, the other four spores are necessarily pF. This accounts for the exact equality of these two types in the above data as well as for the exact equality of the pf and PF classes, for at least one member of each pair of ascospores of each ascus was raised.

The pf ascospores contain the normal allelomorphs of both the *pale* and the *fluffy* genes. The mycelia grown from such ascospores (disregarding *tan*) are identical with the wild-type fungus from which the various mutants were developed. The new double type, *pale fluffy* shows characteristics of both parent types in combination, and is as stable as the parents. It does not form sectors of *pale* or *fluffy*, and, naturally, this would not be expected since both genes have been incorporated into the same nucleus. *Pale fluffy* shows a modification of each of the original types since they now are acting together on the same features of the mycelium.

Each mutant gene was segregated from its normal allelomorph at the first division in some asci and at the second division in other asci. This can be readily deduced from the seriation of the characters in the eight ascospores after they have been raised and classified. Table 4 gives the data on the frequencies of first- and second-division segregation for + versus −, *pale* versus *non-pale* and *fluffy* versus *non-fluffy*. The data on segregation of the sex factors contain additions from crosses other than the one under consideration, while the P/p summary lacks one of the 110 asci.

It has been shown (Lindegren 1932b) that the ratio of first- to second-division segregation of the sex factors is a constant, namely, 87.1:12.9 (corrected by new data). The data in table 4 on the segregation of p from P and f from F show that, in these cases, the ratios are different from that

TABLE 4

Distance from spindle fiber of locus for sex, for pale and for fluffy, deduced from percentage of asci showing second-division segregation

DIVISION	+/−	%	P/p	%	F/f	%
I	391	87.1	73	67.0	42	38.2
II	58	12.9	36	33.0	68	61.8
Distance	6.5		16.5		30.9	

for the sex factors and apparently are specific for each pair of allelomorphs. A consistent explanation, following a suggestion for which the writer is indebted to Dr. E. G. Anderson, can be built up on the basis of the following two assumptions: (1) Crossing-over occurs at the four-strand stage. (2) The spindle-fiber attachment is always segregated reductionally at the first meiotic division (the first division in the ascus). It follows that the percentage of second-division segregation is a measure of the distance of a gene from its spindle-fiber attachment. Second-division segregation of a gene pair would result from single crossing-over of two homologous strands at the four-strand stage between the spindle-fiber attachment and the locus of the gene. This is shown in figure 2. A proof that these two assumptions are true can be obtained by comparing map distances calculated by the ordinary means without reference to the ratio of first- to second-division segregation with map distances calculated from the ratio of first- to second-division segregation. The same data may be used for this comparison since these two methods are entirely independent. This can be seen by arbitrarily rearranging the spores shown in the asci in table 7. For example, all the asci in class 2 could be changed into class 3 as follows:

P+ P− p− p+ (PI; +II) could be changed to P+ p+ P− p− (P II; +I). But any amount of change of this nature would not alter the linkage of *pale* to sex of 22.5 which is shown in table 1. These assumptions then will be demonstrated to be true if the map distance calculated by means of the ratio of first-division to second-division segregation is statistically equivalent to 22.5. As a result of the second divisions each ascus in which such single crossing-over has occurred contains two crossover and two non-crossover chromatids, and, as the result of the third or purely equational

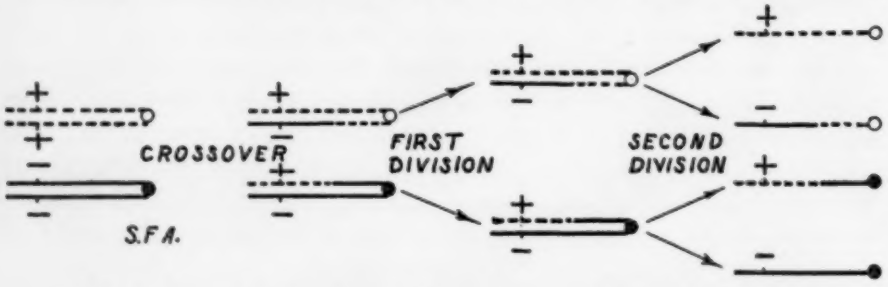

Fig. 2. A diagram to show how single crossing-over between the spindle-fiber attachment (s.f.a.) and the locus of sex (+, −) results in second-division segregation of (+) from (−). At the left, the paired chromosomes are shown at the four-strand stage. Next, the arrangement following crossing-over is shown. The spindle-fiber attachments separate reductionally at the first meiotic division, carrying a + − combination into each of the first two nuclei. At the second-division the spindle-fiber attachments divide equationally, producing the four-nucleate stage, with the nuclei arranged in the ascus in the order in which they are shown in the diagram. Different random orientations of either or both dyads at the binucleate stage would produce other typical second-division segregation configurations. The third (mitotic) division does not change the configuration. The first chromatid corresponds to the first pair of identical ascospores, the second chromatid to the second pair of ascospores, etc.

divisions, four crossover and four non-crossover ascospores. Only half of the pairs of ascospores produced after each second-division segregation contain crossover chromatids. Where all of the ascospores are grown, each case of single crossing-over between the spindle fiber and the locus can be detected. In such diploid organisms as *Drosophila*, one chromatid from each four is sampled and hence in half the reductions in which single crossing-over has occurred, the sample shows a non-crossover chromatid. To express the distance between the spindle-fiber attachment and the locus of a gene in standard crossover units, the percentage of second-division segregation asci is merely divided by 2. This is a method of obtaining certain map distances without dependence on the four class associations of two pairs of linked genes. By this method the distances from the spindle-fiber attachments of the genes for *pale*, *fluffy* and sex were determined, and are

given in the last line of table 4. These values are really "recombination percentages" for the spindle fiber and the gene whose percentage of second-division segregation is being studied. If two cases of crossing-over occurred between this locus and the spindle fiber, the gene would segregate at the first division instead of at the second. Hence, as in the general situation in *Drosophila* and elsewhere, the recombination percentages can be used as map distance only when the distance between the two loci is short enough so that double crossing-over within is negligibly rare. In the case of recombination percentages deduced from second-division segregation, any kind of double within the interval will result in a discrepancy between the recombination percentage and the map-distance. A recurrent double, a progressive double or two independent singles in this interval will cause two crossovers to fail to register as recombinations.

Table 5 shows that with respect to the segregation of the two pairs of genes, P/p and F/f, four classes of asci were found. In class 1, for example, the mutant and the normal genes for both pairs were segregated from each

TABLE 5

Classes of segregation with respect to pale and fluffy, deduced from seriations of pairs of ascospores in 110 asci

CLASS	DIVISION	SUBCLASSES 1&2	3&4	5&6	7&8	NO. ASCI		%	CALCULATED %
1	P/p I	PF	PF	pf	pf	13	29	26.3	25.6
	F/f I	Pf	Pf	pF	pF	16			
	P/p I	PF	Pf	pf	pF	10			
2	F/f II	PF	Pf	pF	pf	15	45	40.9	41.4
		Pf	PF	pf	pF	7			
		Pf	PF	pF	pf	13			
	P/p II	PF	pF	Pf	pf	5			
		PF	pF	pf	Pf	5	14	12.7	12.6
3	F/f I	pF	PF	pf	Pf	2			
		pF	PF	pf	Pf	2			
	P/p II	pf	PF	PF	pf	1			
		PF	pf	pf	PF	1			
		PF	pf	PF	pf	4			
	F/f II	PF	pf	Pf	pF	2			
4		Pf	pF	PF	pf	3	22	20.0	20.4
		PF	pf	pF	Pf	2			
		pF	Pf	PF	pf	2			
		pF	Pf	pF	Pf	2			
		pF	Pf	Pf	pF	3			
		Pf	pF	pF	Pf	2			

other at the first division. Each of the four classes contains subclasses, shown in this table, where the end to end seriation in the ascus is disregarded. In the absence of linkage, each of the two subclasses in class 1 should be present in statistically equal numbers. If the genes were linked, the Pf Pf pF pF original combination asci should be more numerous than the pf pf PF PF recombination asci. Sixteen original combination and 13 recombination asci were found. This approximate equality proves that the genes in question are not linked.

Table 6 shows the classification of 109 asci with regard to *fluffy* and *non-fluffy*, as well as + and − sex. The linkage relations already discussed (table 3) indicate that these genes are not linked. In table 6 the approximate equality of the two subclasses (20 and 16) in class 1 confirms this view.

TABLE 6

Classes of segregation with respect to fluffy and sex deduced from the seriations of pairs of ascospores in 109 asci

CLASS	DIVISION	SUBCLASSES 1&2	3&4	5&6	7&8	NO. ASCI		%	CALCULATED %
1	F/f I	F−	F−	f+	f+	20	36	33.0	33.3
	+/− I	F+	F+	f−	f−	16			
2	F/f I	F+	F−	f−	f+	1			
	+/− II	F−	F+	f+	f−	1	6	5.5	4.9
		F+	F−	f+	f−	1			
		F−	F+	f−	f+	3			
3	F/f II	F+	f+	f−	F−	14			
	+/− I	f+	F+	F−	f−	19	60	55.0	53.8
		F+	f+	F−	f−	13			
		f+	F+	f−	F−	14			
4	F/f II	F+	f−	f−	F+	2			
	+/− II	F+	f−	F+	f−	1			
		F−	f+	F+	f−	2	7	6.5	7.9
		f+	F−	f−	F+	1			
		F−	f+	F−	f+	1			

In table 7, the asci are classified with regard to *pale* and sex, (+) and (−). Correction has been made for reciprocal crosses by reversing the signs for sex in one of the matings. The parental classes are P (+) and p (−). The recombination classes are P (−) and p (+). Sixty-two P(+) P(+) p(−) p(−) asci were found in class 1 and only one P(−) P(−) p(+) p(+) ascus. Therefore, *pale* is strongly linked to the sex-differenti-

ators. We may call the chromosome containing the sex differentiator the sex chromosome, and call *pale* a sex-linked gene. The distance of *pale* from the spindle-fiber attachment is 16.5 (plus an unknown amount due to unobserved doubles). The distance of (+) from the spindle-fiber attachment is 6.5. Here the distance is so short that the correction for unobserved doubles may be very slight. It follows that the distance between (+) and *pale* is either approximately 23.0 (16.5+6.5=23.0) or approximately 10.0 (16.5−6.5=10.0). These are the two possible solutions obtained from data on the percentage of second-division segregation. They are determined in-

TABLE 7

Classes of segregation with respect to sex and pale as deduced from the seriations of pairs of ascospores in 109 asci

CLASS	DIVISION	1&2	3&4	5&6	7&8	NO. ASCI		%	CALCULATED %
	P/p I	P+	P+	p−	p−	62			
1	+/− I	P−	P−	p+	p+	1	63	57.8	58.3
	P/p I	P+	P−	p−	p+	3			
	+/− II	P+	P−	p+	p−	1	10	9.2	8.6
2		P−	P+	p−	p+	3			
		P−	P+	p+	p−	3			
	P/p II	P+	p+	P−	p−	8			
	+/− I	P+	p+	p−	P−	9			
3		p+	P+	P−	p−	7	34	31.2	28.7
		p+	P+	p−	P−	10			
	P/p II	P+	p−	p+	P−	1			
4	+/− II	p+	P−	P−	p+	1	2	1.8	4.3

dependently of the association of *pale* and sex observed in the mycelia developed from the ascospores. Table 3 contains the linkage data. The observed recombination percentage for sex and *pale* is 22.5. This agreement with the expectation of 23.0 proves the validity of the assumptions upon which the calculations of the map distance from the segregation data were based. Therefore, it has been demonstrated that (1) crossing-over occurs in the four-strand stage, and (2) the spindle-fiber attachment is segregated reductionally at the first meiotic division. It is interesting to note the high similarity between the meiotic mechanism in this organism and that in such an organism as *Drosophila*. *N. crassa* is superior in that all the products of each reduction can be accurately known instead of having to be deduced from the sample of one chromatid from each reduction, or two chromatids in the more favorable cases of non-disjunction, attached -Xs, or triploid studies.

Figure 3 is a map of the sex-chromosome, based on the data thus far accumulated, but uncorrected for double crossing-over. Asci in class 2 (table 7) are produced by a single crossover in the (+) arm, which we may call the "left" arm. Asci in class 3 are produced by a single crossover in the

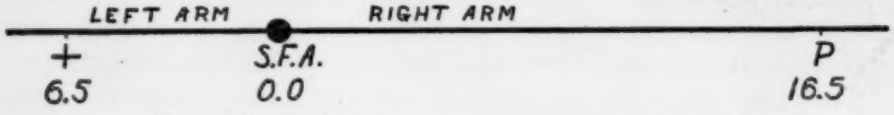

Fig. 3. Map of the sex chromosome of *Neurospora crassa*.

pale or "right" arm. Figure 4 is a diagram showing how this crossing-over would produce asci falling into class 3. The orientation of the chromatids has been given for only a single possibility.

Irrespective of whether genes are linked or independent, it is possible to calculate the percentages of asci falling into each of the four classes by the known percentages of first- and second-division segregation (table 4). The product of the percentage of first-division segregation of P from p (expressed as a fraction) by the percentage of first-division segregation of

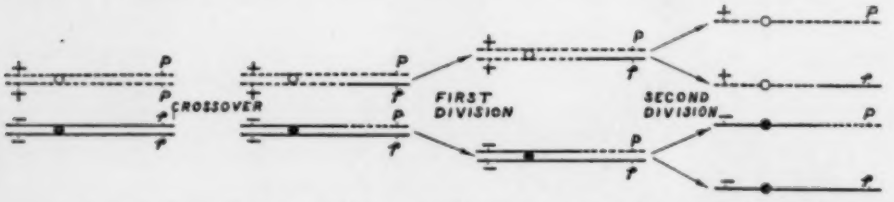

Fig. 4. A diagram to show how crossing-over between the locus of pale (P) and the spindle-fiber attachment (s.f.a.) produces asci of class 3 (table 7). The two homologous chromosomes are shown at the four-strand stage. The first division is reductional with regard to (+) and (−) and equational with regard to (p) and (P). Changes of orientation produce the four sub-classes found in class 3, table 7.

F from f (.670 × .382 = .256) gives the percentage of asci in which both pairs of genes are segregated at the first division, and similarly for the second-division expectation, etc. This has been done in tables 5 and 6 for the independent combinations. In the case of independent genes, the calculation merely involves the assumption that crossing-over in one chromosome has no effect on crossing-over in another chromosome. Although this assumption may not be generally true (Redfield and Schultz in Morgan, Bridges and Schultz 1930), the agreement between the calculated and the observed percentages for these cases indicates that it is correct for the regions involved here.

In table 7 this calculation has also been made. It is important to observe that in the case of linked genes, this calculation involves a different

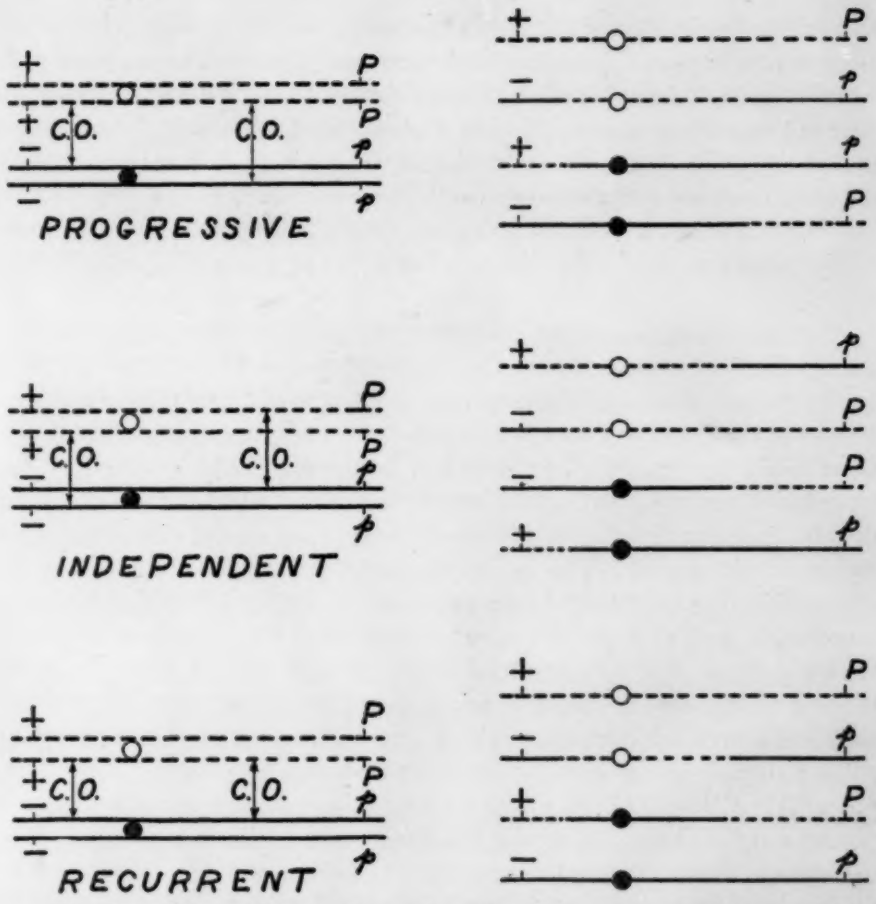

Fig. 5. A diagram showing the configurations of ascospores in the ascus which would result from progressive, independent, and recurrent compound crossovers. The double headed arrows, marked c.o., show the points at which the crossovers occur and the strands involved.

In the diagram of the progressive compound crossover, the upper chromatid at the right (P+) (corresponding to ascospores 1 and 2) is a non-crossover. The second chromatid, (p−) (corresponding to ascospores 3 and 4) is a double crossover. The third chromatid (p+) (corresponding to ascospores 5 and 6) is produced by a single crossover between + and s.f.a. The fourth chromatid (P−) (corresponding to ascospores 7 and 8) is produced by a single crossover between p and s.f.a.

The diagram of the independent compound crossover follows the same scheme. This type is called independent because two different pairs of non-homologous strands cross over with each other. Four single crossover chromatids are produced. In such an ascus, complete reversal of linkage occurs.

In recurrent compound crossover asci, two double crossover and two non-crossover chromatids are produced. The name 'recurrent' is used because the same two non-homologous strands are involved.

viewpoint. In the case of the sex chromosome, the calculation is based on the assumption that a crossover in one region of this chromosome does not interfere with a second crossover in an adjacent region, but that crossovers are distributed at random, without "interference." Since the two regions are on opposite sides of the spindle-fiber attachment, this may very well be true, even for loci close together. The agreement in the case of the linked genes is not so close as in the case of the independent genes, but the numbers are too small to be significant as to the presence of an interference effect.

The asci found in class 4 and the recombination ascus in class 1 are produced by two crossovers in the sex chromosome. Those in class 4 will be designated compound-crossover asci to distinguish them from double-crossover chromatids. These compound-crossover asci can be divided into three main groups, called progressive, independent and recurrent. One progressive and one independent were found. The progressives contain one double-crossover chromatid, one non-crossover chromatid, and two single-crossover chromatids. The independents contain four single-crossover chromatids. The recurrents (none was found) contain two double-crossover chromatids and two non-crossover chromatids. The calculation of the expected percentage of compound-crossover asci, on the assumption of random distribution of crossing-over, is made by taking the product of the fractions representing second-division segregation (not the fraction representing the amount of crossing-over) for each region involved. For example, $.330 \times .129 = .0426$. As already stated, the numbers are too small to permit conclusions regarding the significance of an interference effect. The calculation of the expected percentage of double-crossover chromatids is made according to the method commonly used by taking the product of the fractions representing the two adjacent map distances. For example, $.065 \times .165 = .0107$. Let us say that roughly 4 percent of compound-crossover asci (segregation method) and 1 percent of double-crossover chromatids (linkage method) are calculated. Then, to take a concrete example, 4 asci in every 100 asci should be compound-crossover asci. One hundred asci contain 400 chromatids. Therefore, 1 percent, or 4 chromatids out of 400 chromatids, should be double-crossover chromatids. If the two methods of calculation (segregation and linkage) are in agreement, four compound-crossover asci should, on the average, contain four double-crossover chromatids. It is planned to test this point with larger numbers.

The recombination ascus in class 1 (table 7) is capable of two explanations (fig. 6). It could result from two simultaneous independent-crossovers between *pale* and the spindle-fiber attachment, or by two simultaneous independent-crossovers between (+) and the spindle-fiber attachment.

The *pale* parent used in the above cross was genetically *tan* as well. In the progeny the *fluffy* (pF) mycelia could be classified into two groups: *fluffy tan* (pFT) and *fluffy non-tan* (pFt). The *non-pale non-fluffy* (pf) progeny could also be classified with respect to *tan*. Both *tan* (pfT) and *non-tan*

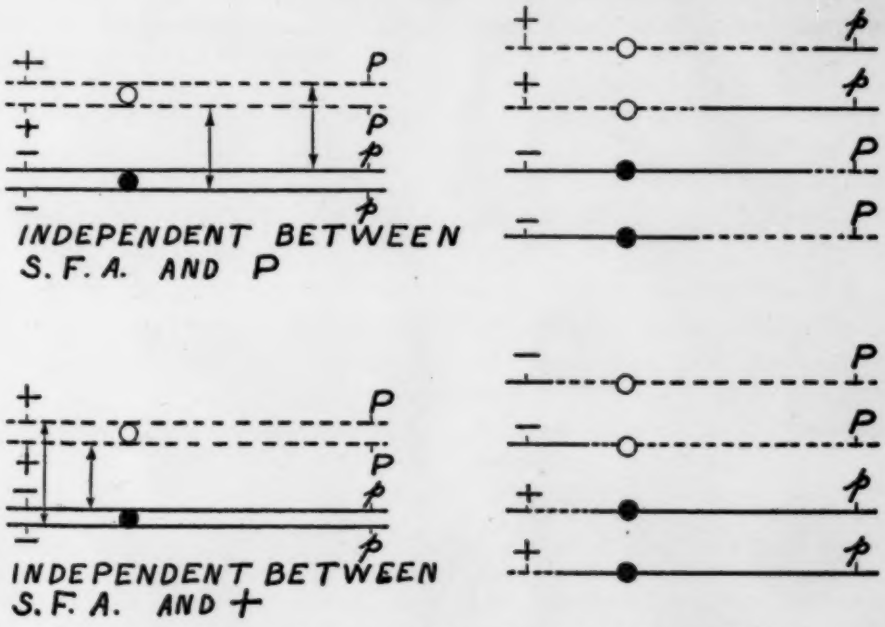

Fig. 6. A diagram showing two possible explanations of the recombination ascus in class 1 (table 7).

(pft) were found. In both cases, the *tan* and *non-tan* classes occurred in equal numbers. This proves that *tan* is not linked to either *pale* or *fluffy*. *Pale* and *pale fluffy* mycelia could not be classified into *tan* and *non-tan*.

SUMMARY

The development of six stable pure bred stocks and one constantly mutating stock is described. It is suggested that the stable stocks were produced by the segregation of modifying genes from the genes differentiating the stocks. The stability of these six stocks, and the fact that the constant mutation is apparently at a single locus, suggest that most of the genes in this fungus are stable. It is suggested that many of the apparent mutations in fungi may be due to "Dauermodifikationen" and the selection or destruction of one nucleus in a heterokaryon, rather than to "point mutations."

Evidence is offered indicating (1) that the ascus nucleus in *Neurospora*

crassa is diploid; (2) that the reduction of the diploid nucleus to four haploid nuclei is effected in the first two divisions of the ascus nucleus; (3) that crossing-over occurs at the four-strand stage; (4) that the spindle-fiber attachment is segregated reductionally at the first meiotic division.

A three-point map of the sex chromosome is constructed, and the types of crossing-over in the two adjacent regions are discussed.

The writer is grateful to Dr. T. H. Morgan for his continued interest. He has enjoyed the privilege of discussing the problem with Dr. Albert Tyler, Dr. E. G. Anderson, Dr. Calvin B. Bridges, Dr. S. H. Emerson, and Dr. A. H. Sturtevant. He is particularly indebted to Dr. Bridges for his helpful revision of the manuscript, and to Dr. B. O. Dodge for editorial criticism.

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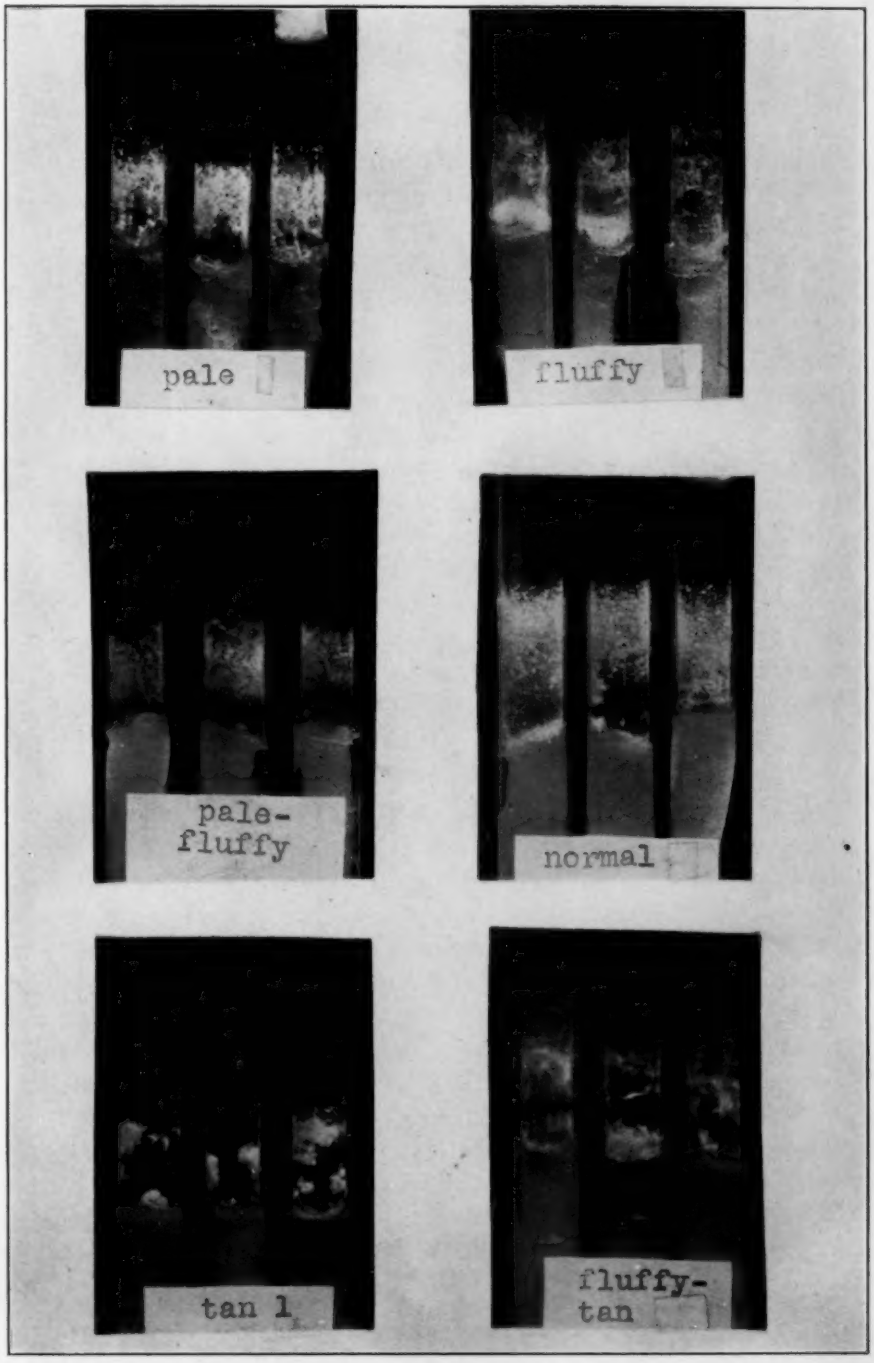

LINDEGREN: NEUROSPORA

UNIV. OF MICH.

Autogamous Turkestan rye

BASIL M. BENSIN[1]

(WITH THREE TEXT FIGURES)

This new species of rye was discovered by the writer in 1912, while engaged in an expedition organized by the Russian Bureau of Applied Botany for the investigation of Turkestan cereals, chiefly in their relation to drought-resistance. It was found in cultivation in the field of a Kirghizian farmer by the name of Dair Barzabaeff, about ten miles from Aulie-Ata, in Syrdaria Government.

According to native Kirghizians, this type of rye appeared in comparatively recent times mixed with the wheat, gradually becoming a dominant plant in the wheat-fields. The local Kirghizian name for it is Kara-bidaj ("black wheat"), and they supposed that their white wheat (Ak-bidaj) gradually degenerated into black wheat (Kara-bidaj), not realizing that the plant was actually rye. It was sold in the market at Aulie-Ata, in 1912, at the same price as wheat: 1 ruble per pood or about $1.00 per bushel.

The local wheat consists entirely of early varieties: white wheat (*Triticum vulgare* var. *graecum* Körn.) in very many forms, and durum wheat (*Triticum durum* var. *hordeiforme* Host). Both of these species have light-colored kernels, white or yellow, so the dark brown kernels of the new species of rye were quite conspicuous in the lots of grain.

The rye is thus replacing the wheat as a crop plant, apparently because it is better adapted to the local climatic and cultural conditions (agrochora). We have here a case of competition, in cultivation, between two crops, the better-fitted becoming dominant. The yield of the rye, however, was not very high; it was said to amount to about 50 poods per desiatin (12.3 of a bushel per acre) on irrigated land. Only locally home-made plows are in use.

The author described this Turkestan rye in a report on his Turkestan trip, published in the Bulletin of the Bureau of Applied Botany in 1913, with illustrations but without a formal name or Latin diagnosis.[2] On the basis of morphological characters and geographic distribution he regards

[1] The author wishes to thank Dr. H. A. Gleason and Dr. J. H. Barnhart of The New York Botanical Garden for the encouragement and kind assistance in preparation of this article and to Dr. E. D. Merrill who made it possible to publish it.

[2] Benzin, B. M. The notes on my Turkestan trip. Bull. Angew. Bot. 1913: 459–495. 1913. (Russian, with English résumé. Reprinted in Russian, with slight alterations and a changed title, Tashkent, 1915.)

it as a distinct species, and as an agroecological xerophytic chorotype, and accordingly here supplies it with both name and diagnosis:

Secale turkestanicum Bensin, sp. nov., spiculis semper trifloris, floribus omnibus aut ullis 2 fertilibus; lemmatibus latis ad basin carinatis; paleis ad lemmata etiam usque ad maturitatem arcte adhaerentibus et floribus ergo autogamis; rachide basi albopiloso rigido nec fragile; granis oblongis basi acute carinatis atro-brunneis aut basi paene nigris firmissime adhaerentibus neque ad maturitatem diffractis. Habitat in valle fluviorum Talas et Chu, cultum, prope Aulie-Ata, Sirdaryatan, Turkestan, Asia centralis.

Turkestan rye has the spikes usually about twice as long as in ordinary cultivated rye; the long rachis very stiff but not fragile, conspicuously villous at the base of each spikelet.

There are always three flowers in each spikelet, which are designated in the accompanying figure as f, f_1, and f_2. Sometimes all three bear fruit, but commonly this is true of only two (f and f_1, f and f_2, or f_1 and f_2); in the first case, the uppermost flower is smaller. The lemma and palea are so closely appressed to each other that the flower can not open during pollination, so it is evident that this species is self-pollinated (autogamous).

The kernels are more elongate than in ordinary rye, *Secale cereale*, and are much narrower and pointed at the base, where the embryo is situated. They are dark brown above and black below. They are firmly attached at the base, and are so completely covered by the lemma and palea that they are hidden even when fully mature and dry, consequently they do not shatter, as does ordinary rye.

The most essential differences from ordinary rye have been indicated above, but may be here summarized: (a) invariable development of three flowers instead of two in each spikelet; (b) frequent maturity of the fruit of the uppermost flower; (c) complete enclosure of the flower in the lemma and palea, and consequent self-pollination, instead of an open flower with cross-pollination; (d) firm attachment of the kernels and consequent non-shattering upon maturity, instead of easily shattering kernels; (e) stronger development of villous hairs at the base of each spikelet; (f) dark, almost black, color of the kernels.

Agroecological features. This rye chorotype of Turkestan possesses distinctly xerophytic adaptations. The protection of its pollen with the resulting autogamy is a striking adjustment to its climatic environment, which is characterized by dry south-eastern winds. The protection afforded to the spikelet by the villous hairs at its base is another xerophytic character.

The firm attachment of the kernels is also important from an agroeco-

Fig. 1. *Secale turkestanicum* Bensin. Natural size of fully mature ear.

logical standpoint, in a region where agriculture is poorly developed and there is no harvesting machinery except the sickle and the scythe. The crops mature more rapidly than they can be harvested, and the Kirghizians would lose more than three quarters of the yield if they grew ordinary rye, with its strongly shattering kernels.

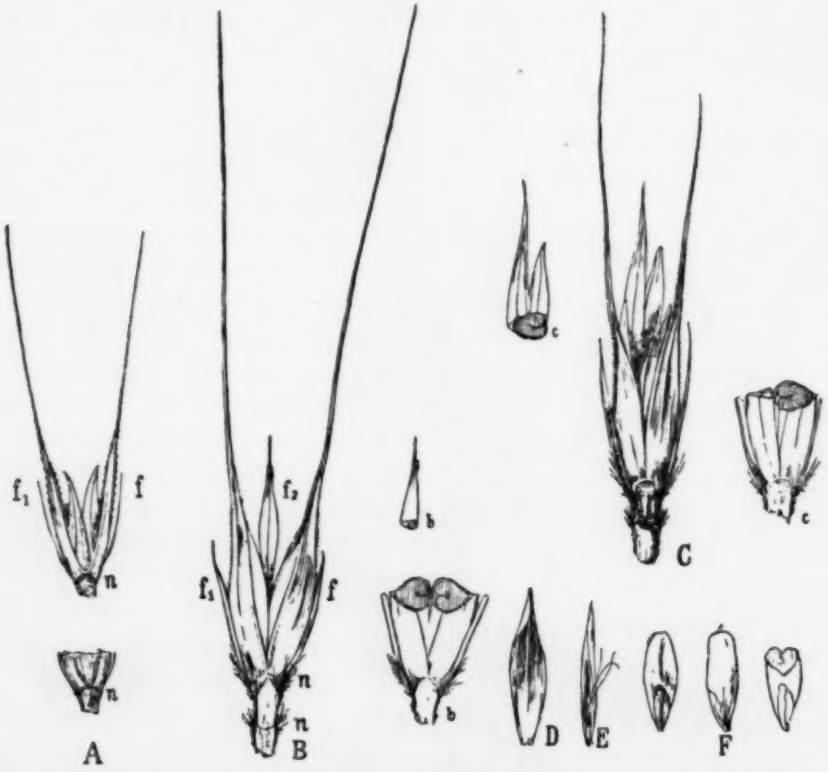

Fig. 2. *Comparison of Secale turkestanicum with S. cereale.* A. Spikelet of *Secale cereale* L. f, f_1, two flowers; n, glabrous base of spikelet. B. Spikelet of *Secale turkestanicum* Bensin. f, f_1, f_2, three flowers; n, hairy base of the spikelet; c, section of lower fruiting and one upper flower. C, spikelet with fruiting lower and upper flower. D, palet of fruiting flower. E, palet of unfertilized flower. F, kernel.

Previous records of rye with 3-flowered spikelets. In 1812, Palisot de Beauvois[3] named as a new species *Secale triflorum*. All he says about it is: "J'ai trouvé cette dernière espèce à Dunkerque sur les bordes d'un nouveau canal qui conduit à la mer. Elle ne diffère du *S. cereale* que par la troisième

[3] Palisot de Beauvois, A. M. F. J. Essai d'une nouvelle agrostographie. 1–182. 1812. (*Secale triflorum* on page 105.)

fleurette." It is evident from his generic description that the third flower was sterile.

In 1857, Döll[4] described a variety of ordinary rye, *Secale cereale* var. *triflorum*, "Aehrchen mit lang gestielter dritten Blüthe," as not rare in wet seasons as solitary specimens in various places in Baden. His generic description, however, shows that the third flower, when present, was rudimentary.

In 1881, Regel[5] described in few words an Asiatic plant that he regarded merely as a variety of ordinary rye, under the same name, *Secale cereale* var. *triflorum:* "spicula triflora, flore supremo pedicillato masculo. Colitur in Chiwa."

In 1885, Körnicke, discussing[6] abnormalities of development in rye, devotes nearly half a page to the occurrence of 3-flowered spikelets. He cites Palisot de Beauvois, Döll, and Regel, commenting upon the rarity of specimens with three fertile flowers, and mentions one record of spikelets each of which produced four perfect kernels. These were all, however, in other respects ordinary rye.

Relation of S. turkestanicum to S. cereale. While *S. turkestanicum* has a local and limited distribution in Turkestan, being an endemic Turkestan plant, it may shed light upon the relationship between *Secale* and other genera of Gramineae, especially the cultivated ones *Hordeum* and *Triticum*. I assume that it is a more primitive species than *S. cereale*, which has probably been derived from it during the centuries since rye was first cultivated in Asia and Europe. It is rougher, with the flowers in the spikelets unevenly developed, but is better adapted to a wild state, where it grows scattered and isolated, and is more resistant to drought, while *S. cereale* is more highly specialized, and is adapted to a milder climate and better cultivated fields.

We might compare *S. turkestanicum* with *Triticum polonicum*, which it resembles, and with *Hordeum hexastichum*, also with three developed flowers. These three would form a series of more primitive species than *S. cereale*, *T. vulgare*, *H. distichum*, as may be graphically illustrated by the following table.

[4] Döll, J. C. Flora des Grossherzogsthums Baden. 1–1429. 1857–62. (*Secale cereale* var. *triflorum* on page 122.)

[5] Regel, E. A. von. Descriptiones plantarum novarum et minus cognitarum. Fasciculus VIII. Acta Horti Petrop. **7:** 541–677. 1881. (*Secale cereale* var. *triflorum* on page 579.)

[6] Körnicke, F. A. Die Arten und Varietäten des Getreides. (In Körnicke & Werner. Handbuch des Getreidebaues.) 1–470. *pl. 1–10.* 1885. ("Bildungsabweichungen" on pages 119–121.)

	Hordeum	Secale	Triticum
Primitive species.	*hexastichum*	*turkestanicum*	*polonicum*
Specialized species.	*distichum*	*cereale*	*vulgare*

Secale turkestanicum thus lessens the gap in the relationship between the genera *Hordeum*, *Secale*, and *Triticum*, which have had such an enormous influence in the history of agriculture and of human culture.

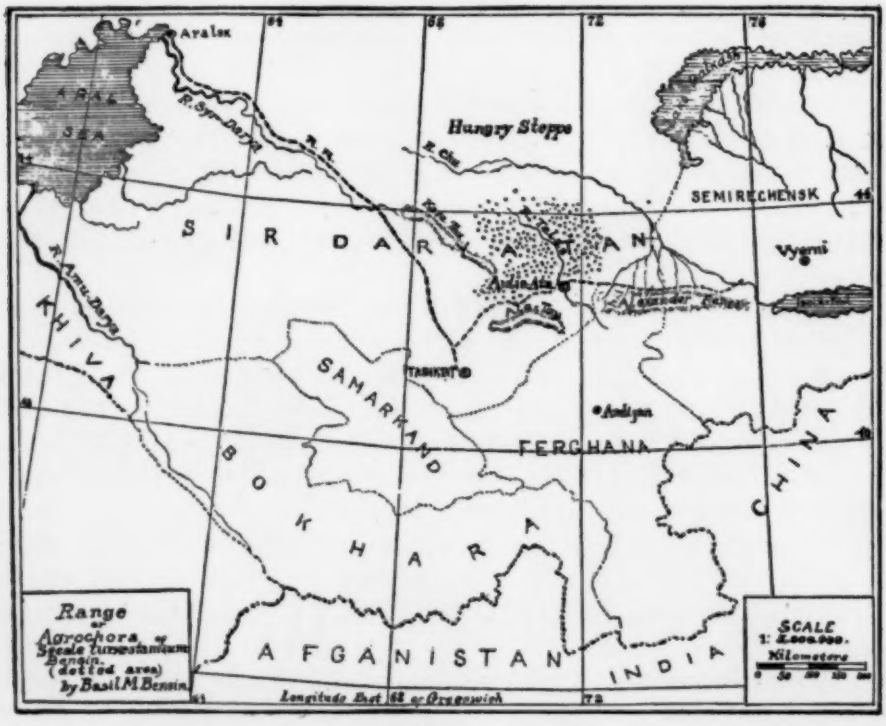

Fig. 3.

Unfortunately, I have no prospect of being able to make further detailed studies and experiments with *S. turkestanicum*, which would be such an interesting subject for plant-breeding work and agroecological investigations in the arid and subtropical regions.

NEW YORK CITY

A review of recent work on the effect of ultraviolet radiation upon seed plants

H. W. Popp and Florence Brown[1]

INTRODUCTION

Prior to 1927 it had generally been conceded by those who had examined carefully the experimental evidence available, that ultraviolet radiation, particularly the shorter wave lengths, was inimical to higher plants. Since 1927, however, numerous papers have appeared in which an apparent effort has been made to demonstrate beneficial effects on higher plants comparable to those reported as occurring in the animal organism. These beneficial effects as a rule have not been very outstanding. Unfortunately many of the papers report the results of extremely short experiments without adequate controls, carried out with so few plants as to render the conclusions extremely doubtful. In no case has the ultraviolet to which the results have been attributed been the only variable in the test plants as compared with the controls. So long as this is true results obtained in such experiments will be of little value no matter how many of them may be reported in the future. Indeed, it may truthfully be said that such papers thus far have done more harm than good because of the acceptance of the erroneous conclusions by the average reader who has no time to examine the data critically. Perhaps even more serious is the fact that these extremely doubtful conclusions have been quoted without criticism again and again in later scientific papers, indicating that a thorough and critical examination of the experimental procedure and the results obtained in the earlier papers could not have been made. It cannot be overemphasized that valuable results in this field can be obtained only by long-continued experiments under accurately controlled conditions.

The aim of this discussion is to present a critical review of the work that has been done on the effects of ultraviolet radiation upon seed plants, with particular emphasis on the work of recent years up to the early part of 1932. The subject is subdivided as follows:

Part I. The effect of ultraviolet radiation upon seed germination and early growth of seedlings.

Part II. General and specific effects of ultraviolet radiation upon more mature plants.

Part III. Other effects of ultraviolet radiation upon seed plants.

[1] Contribution No. 80, Department of Botany, The Pennsylvania State College, State College, Penna. Publication authorized by the Director of the Psnnsylvania Agricultural Experiment Station, Technical Paper No. 568.

PART I

THE EFFECT OF ULTRAVIOLET RADIATION UPON SEED GERMINATION AND EARLY GROWTH OF SEEDLINGS

Before 1921 very few investigations had been carried out on the effects of ultraviolet radiation upon seed germination and early growth of seedlings. Carl (24) had stated that ultraviolet rays from a mercury vapor lamp were detrimental to seed germination and the early growth of plants. Raybaud (114, 115) on the other hand, had reported that the rate of germination of certain seeds was increased by such radiation, but that the seedlings were injured and died soon after emerging from the seed coats. Schanz (128) had found that seeds did not sprout as readily in daylight containing ultraviolet radiation as in daylight from which this radiation was screened out.

In 1921 Popp (106, 107) carried out investigations upon the effect of ultraviolet radiation upon seed germination and early growth of seedlings. In a series of experiments upon various types of seeds including foxglove, tobacco, mustard, corn, Canada field peas, lupine, and sunflower he made numerous tests using the mercury arc in quartz as the only source of radiation. In some cases it was used unscreened and in others screened by various filters. The length of exposure ranged from a total of one or two hours up to six to ten hours per day for several days. The ranges of radiation reaching the experimental plants were indicated by spectrograms. From 50 to 100 seeds were used in each test with a corresponding number of controls, involving a total of about 5,000 seeds. Plants were compared which had received approximately only the region 420 to 320 mμ. plus some infra-red, only the visible and infra-red plus the ultraviolet down to 300 mμ., and the visible and infra-red plus the ultraviolet down to about 200 mμ. Intensity differences under the various experimental conditions were not recorded because instruments for measuring these were not available.

The experiments indicated that exposures of dry seeds to the entire radiation of a quartz mercury arc for as long as 188 hours had no effect on later germination and growth and that exposures of less than two hours of soaked seeds that had not yet begun to sprout had no effect on later germination and growth. This was explained as probably due to the failure of the short injurious rays to penetrate sufficiently to be effective. Longer exposures of soaked seeds were injurious, and wave lengths below 300 mμ. were particularly harmful. No differences in rate of germination were noted in seeds grown in the dark, in the radiation of the lamp from which the ultraviolet was screened off, or under the lamp from which only

the ultraviolet below about 300 mμ. was screened off. If, however, the principal radiation (aside from infra-red) the seeds received was ultraviolet of the approximate region 400 to 300 mμ., injurious effects were indicated, more upon the seedlings after germination than upon the rate of germination, but these effects were probably chiefly caused by the absence of sufficient light for growth. Seedlings grown with the unscreened lamp as the only source of radiation never developed beyond the stage that would result from food stored in the seeds. This, plus the fact that starch tests on mature geranium leaves which had been irradiated, were negative, was thought to be an indication that food synthesis is slight under the radiation of the unscreened lamp.

From 1921 to 1927 the reports of Sibilia (145), Russell and Russell (123), Dane (30), and Ritson (37) all indicated only injurious effects of the unscreened mercury vapor arc. Ritson's conclusion that germination of *Trifolium subterraneum* is delayed by short repeated exposures to the unscreened arc is hardly justifiable since the seeds were planted in the soil where ultraviolet radiation obviously could not have reached them. His observations on the seedlings after they had appeared above ground are, of course, not open to this criticism.

Beginning in 1927 Sheard with various co-authors published a number of papers on the effect of "general" and "selective" irradiation upon plants. Four of these (135, 67, 136, 137) deal with germination of seeds and early growth of seedlings. Since we find the conclusions of these authors repeatedly referred to as though they were established facts, it seems desirable to call attention to the manner in which they were reached. One is led to wonder whether those who have accepted the conclusions of these authors could have examined their papers critically.

In general the papers may be characterized as consisting of a minimum of experimental data on exceedingly few plants from which a maximum of conclusions and generalizations are drawn. In the four papers a total of 21 conclusions is reported. Of these the one most frequently quoted (67, conclusion 3) states that "wave-lengths ranging from about 320 mμ. to 390 mμ. seem particularly effective in inducing growth." The experimental data upon which this conclusion is based are recorded in the only table in this paper. A series of ten cultures, each containing six to ten cucumber seeds had been observed for about eight days. One of these cultures had been given short daily exposures to the full spectrum of a mercury arc in quartz, and hence received radiations as low as 200 mμ.; one had been given daily exposures to the mercury arc screened by ordinary window glass which was said to transmit rays down to about 320 mμ.; one had been given daily exposures to the mercury arc screened by vita glass which

transmits down to 270 mμ.; and one had been given daily exposures to the mercury arc screened by ultra glass which was said to transmit only the region 320–390 mμ. These, with a fifth control culture, were otherwise kept in the diffused light of a greenhouse as transmitted by the various screens with which they were covered. The control culture and the unscreened arc culture as well as the window glass culture had a window glass cover while in the greenhouse. The other five cultures paralleled the first five except that they were kept in darkness instead of in diffused light. Length of seedlings was the sole criterion by which the plants were judged. The longest seedlings were assumed to have been under the most favorable conditions. While the experiment was said to have been repeated five times, the data given are stated to be only "sample data which correctly portray the results which were found to occur under the experimental conditions cited in at least 80 per cent of the cases." Anyone who has worked extensively with ordinary vegetable seeds, and particularly with cucumber seeds, knows that such seeds even under constant environmental conditions, exhibit wide variation in the rate of growth during the first few days of germination. Consequently data obtained from a quantity of six to ten seeds have little significance. The data given indicate, however, that the seeds under ultra glass did start to germinate a little earlier than any others. Yet the control culture in the dark not only overtook both ultra glass cultures but by the eighth day the length of these seedlings had exceeded by 12 mm. the length of the ultra glass seedlings kept in the dark, and by 42 mm. or over 100 per cent the length of the ultra glass seedlings in diffused light. The latter fact is overlooked by the authors. If the region 320–390 mμ., the only region except infra red which is transmitted by the ultra glass, were beneficial, and if length of seedlings could be considered as a criterion of stimulation, as it was by the authors, it would seem that those seedlings receiving this radiation should have been longer than seedlings otherwise similarly treated except that they did not receive this radiation. Moreover, the ultra glass culture in diffused light supposedly received nothing but the region 320–390 mμ., but more of it than the one in the dark, since it also received this region of ultraviolet in daylight as well as that present in the mercury arc spectrum. Yet the diffused light ultra glass seedlings were much shorter, only 57 per cent as long as those of the corresponding dark culture. The ultra glass diffused light culture could not, of course, be compared with the control in diffused light since the former received no visible rays and hence was etiolated as compared with the diffused light control which was not etiolated. It is difficult to understand how it could have been concluded from these data that the region 320–390 mμ. was beneficial, even if the data were significant. Such

differences as are recorded are apparently different degrees of etiolation resulting from differences in total radiation, temperature, etc., etiolation being considered as "stimulation."

Conclusion 4 of this same paper (67) is the next most frequently quoted one. It states that "wave lengths of 270 mμ. to 320 mμ. appear to be inhibitory in their action." This is based upon the fact that the seedlings under vita glass were never as long as comparable seedlings under ultra glass. This "lessened growth" was ascribed in the discussion of the paper as due either to the "inhibiting effect of the visible light or the lethal effect of the lesser wave-lengths" transmitted by vita glass and not by ultra glass. In the conclusion, however, the possibility of the significance of the visible rays has been dismissed. In other words, lack of etiolation due to the presence of visible rays is interpreted as inhibiting action of the ultraviolet in the region 270–320 mμ. It might be stated that while evidence from the accurate work of others does indicate that ultraviolet of wave lengths shorter than 300 mμ. is inhibitory to plant growth, the data of these authors are in no sense a proof of it.

In paper 4 (137) we have the statement that "the infra red and red regions of sunlight, at one end of the spectrum, and the blue, violet and ultra-violet at the other extreme of the solar spectrum, are vital and stimulating to growth," and that "growth is greater under either the longer or the shorter wave-lengths of sunlight than it is under the full complement (practically) of sunlight." These statements are made without a single item of experimental data to support them; that is, *no data are given*. Even if we are to assume that the number of plants used and the methods employed were the same as in their papers that do give experimental conditions such conclusions are simply absurd.

Without going further into the remaining conclusions of these authors, suffice it to say that they are supported by no better evidence than the ones mentioned. Thus far Delf (36) is the only worker who has offered any specific criticism of the Sheard and Higgins reports. Delf has mentioned in a general way the disregard of light intensity differences.

In addition to the Sheard and Higgins reports about ten other papers since 1927 have reported favorable effects of ultraviolet radiation upon seed germination and early growth of seedlings. Ordinarily this might be interpreted as piling up of evidence in support of the original conclusion. That such is not the case, however, is clearly revealed by a careful examination of the papers themselves. Unfortunately misconceptions with small beginnings tend to grow as readily as correct ideas.

Brief reports in Gardeners' Chronicle for 1927 and 1928 by Maddock (81), Russell (122), and the Kew Gardens (70) state in general that better

results were obtained in houses covered with the English vita glass, which transmits all wave lengths of daylight ultraviolet, therefore down to 291 mμ., than in houses covered with ordinary window glass, which transmits only down to about 313 mμ. Vita glass is one of a number of glasses which have been put on the market since the region 291 to 313 mμ. has been thought to be beneficial to higher animals. It is described in greater detail in the last subdivision of Part II of this review. The source of radiation in these experiments was daylight only. Russell states that seeds and seedlings when screened with vita glass germinated earlier and showed taller and sturdier growth than did those under ordinary glass, but no definite data are given in his report. In the Kew Gardens report it is stated, regarding germination that "the first lap of the race between two sets of seeds and plants . . . has ended in victory by twenty-four hours for those grown under the new glass which admits the ultra violet rays of the sun." Whether or not the seed stimulation refers to seeds which were planted is not stated. In addition, the mistake made in these papers is that of attributing the results to one variable, ultraviolet, when many other variables such as temperature, total radiation intensity, visible radiation, and infra-red radiation, also existed.

Valentin's experiments (166) were similar to those with vita glass reported above, except that he used Ultravit glass, a German product, instead of vita glass, to transmit all wave lengths of daylight ultraviolet. He compared school children, various chemicals, and the germination and growth of plants in two school-rooms having Ultravit glass windows, with those in two schoolrooms having ordinary glass windows. Corn, oats beans, and peas were put in each school room, eight seeds per room. These were planted in flower pots equally deep in the soil. ("Die Samen wurden gleichmässig tief in die Erde gebracht".) Because the seedlings in the pots behind Ultravit glass appeared above ground sooner than those behind window glass the conclusion of the author was that the earlier appearance of the one set of seedlings was due to stimulation of germination by the ultraviolet transmitted by Ultravit glass and not by window glass. It is difficult to understand how any ultraviolet could possibly have reached seeds buried in soil. Yet this obviously erroneous conclusion has been quoted by Masure (87) without comment. Further growth of the seedlings was somewhat better behind Ultravit glass than behind window glass. Additional comment on this is unnecessary.

Jacobi (68), after giving an extensive review of literature dealing with general effects of ultraviolet radiation, presents the results of his own experiments, some of which were concerned with seed germination. Radish, mustard, and lettuce seeds were selected for this work because they ordi-

narily give better germination in the dark than in the light. A mercury vapor lamp was used as the source of radiation. By the use of glass and solution screens, all other regions of the spectrum were eliminated, except the region between 300 and 400 mμ. When dry seeds were exposed to this region for periods of 8, 16, 24, and 32 hours, no marked effect was produced on germination except that the mustard irradiated 24 hours and the lettuce irradiated 32 hours seemed to be furthered in growth after two days. Soaked seeds, on the other hand, irradiated for 2, 4, 6, and 8 hours were reported to give a somewhat higher rate of germination. Exposures of soaked seeds for 10 hours reduced the rate of germination. Seeds irradiated after the emergence of the radicle were unaffected by 2, 4, 6, 8, or 10 hour irradiations.

An examination of the data in which favorable effects of the radiation seem to have occurred shows wide variations and fluctuations in the rate of germination of irradiated plants as compared with controls. For example, after 66 hours the average percentage germination of lettuce irradiated for 2 hours was 65.5 while that of the control was 63.75 per cent, but this same seed irradiated for 4 hours gave 63.5 per cent germination in the same time, while the control gave 68.5 per cent. Furthermore, there is no consistent correlation between time of irradiation and effect. In one instance the 2-hour exposure gives the highest rate; in another the 6-hour one; in still another, the 8-hour one. While in many cases the controls were somewhat behind the irradiated plants in rate of germination, fluctuations are so great that it would hardly be justifiable to attribute this to a stimulating effect of the region between 300 and 400 mμ.

Mezzadroli and Vareton (93, 94) claim to have obtained favorable results on germination and the first stages of seedling growth by irradiating in an oblique direction, with ultraviolet of wave lengths 330 to 390 mμ., obtained by screening a mercury arc with Wood's filter. The favorable effects were scarcely noticeable the first day, most conspicuous during the first days of seedling growth and diminished after about the tenth day. Although the authors report that numerous experiments were carried out on diverse plants for varying lengths of time, they give only four examples. One hundred barley seeds, 50 kidney beans, 25 peas, and 25 corn grains were irradiated 30 minutes per day at a distance of 50 cm. from the light source in an oblique direction. Of these only 41 barley seeds germinated, 30 kidney beans, 23 peas, and 13 corn grains. In the corresponding controls 31, 25, 19, and 10 seeds respectively germinated. It is difficult to understand why seeds giving such low percentages of germination should have been used in the first place. Measurements obviously were made on very small numbers of plants. Moreover there is no indication that en-

vironmental conditions aside from quality of ultraviolet radiation were equalized between experimental and control plants. In the experiment with the most seedlings there is practically no difference in average lengths of seedlings under the two conditions. The measurements are 48.8 mm. for irradiated and 48.4 mm. for non-irradiated seedlings. When fewer seeds were used the differences in average lengths of seedlings were greater, but it is doubtful that these differences were due to irradiation treatments. Average fresh weights of tops of seedlings at the end of 12 days for the control plants were uniformly as good as or better than those for treated plants. In the table published total lengths and total weights of seedlings are given, which might be misleading, since different numbers of measurements make up the totals in each case.

In a second paper are presented effects of the unscreened lamp. In general, damaging action of this treatment was noted, but at a distance of 50 cm. from the light source in an oblique direction with daily doses of one to five minutes duration, a slight excitation was noted, especially in plants kept in darkness. If the time of exposure was increased, instead of more marked favorable effects, the treatment caused injury. There is nothing very conclusive about these results, and the authors themselves are not very emphatic in their support of this method of obtaining favorable effects on seedlings.

Popoff (105) in his book on "Die Zellstimulation" reports general increase in rate of germination and better development of seedlings of rye and wheat under short exposures to an unscreened mercury vapor lamp. This "stimulation" in the case of soaked wheat seeds meant 96 per cent germination in the test plants as opposed to 92 per cent in controls. In other cases the differences were somewhat greater though of little practical significance. In any case, the conditions of the experiment indicate no provision for differences in environmental conditions aside from ultraviolet radiation, but the results are ascribed exclusively to ultraviolet radiation. Incidentally the author likewise finds that seeds are stimulated by chemicals, electricity, high frequency currents, radium, x-rays, hormones, and by various other means.

One of the most recent papers in which stimulation of early development of seeds is claimed is that of Masure (87). He has watched the behavior for four days of pea seeds kept in the dark after irradiation for various lengths of time with a mercury vapor arc in quartz through a Corning G586AW screen. The range of this filter was given as 3334 to 3690Å. with a maximum transmission in the region 3650Å.

In the introduction to this paper Fuller (49) is quoted as having tested some of the work of Popp and Brown and obtained considerable increase

in growth where they obtained negative results. Fuller's work, however, cannot be compared with that of Popp and Brown because the conditions under which his experiments were conducted were entirely different from those of the latters' experiments. Furthermore, Fuller worked with more mature plants whereas Popp and Brown, in the work cited, dealt exclusively with the effect of ultraviolet radiation upon seed germination and the early growth of seedlings. Fuller has in no way repeated the work of Popp and Brown.

In the summary of the paper only the possible demonstration of stimulation is mentioned, although earlier in the paper the author gives data which he himself states as indicating lack of stimulation. For instance, under no conditions of exposure in which the rate of germination was recorded did the irradiation of dry or soaked seeds influence in any significant degree the rate of germination. As stated by the author, "The results obtained allow only one conclusion to be drawn, namely, that raying has no marked effect on the rate of germination." Moreover, the data including average hypocotyl lengths of seedlings subjected to statistical analyses "do not indicate that the raying had a distinctly significant effect on the seeds."

The author's statistically significant figures indicating stimulation were obtained by comparing frequency distributions of root growth of seedlings of related pairs of lots of rayed and control populations. In this comparison the frequency distribution curves for a treated and a corresponding control lot were plotted on the same sheet of graph paper, and a comparison made of the shift of the treated relative to the control population. By thus abandoning "average growth values" as masking the effect of raying and resorting to statistically analyzed frequency distribution curves of root growth, he has obtained significant figures in favor of raying; that is, the percentage number of seedlings of rayed lots growing as fast as the fastest third of control lots was greater for rayed groups. While the statistical methods used seem to be satisfactory, the author has failed to give the data which would enable one to determine actual population distributions, upon which his only demonstration of stimulation is dependent. Furthermore, it cannot be overemphasized that while statistical analyses may show significant differences between test plants and controls, no statistical method in any sense indicates that one of a multiple of operating factors is the sole cause of the significant difference unless all of these factors are taken into account.

That variations between test plants and controls other than the presence or absence of ultraviolet radiation did occur in Masure's experiments is very probable. Certain measurements of the radiation used by Masure,

made in our laboratories with a Kimball and Hobbs pyrheliometer, indicate this. A sample of G586AW glass of the type used by Masure gave a total transmission of 10.71 per cent of the radiation from a Cooper Hewitt mercury vapor arc. When a sample of Noviol "O" glass was interposed between the mercury arc and the G586AW screen the transmission was 7.14 per cent of the energy incident on the Noviol "O" screen. Since the Noviol "O" glass transmits practically no ultraviolet, the 7.14 per cent transmission of these two glasses together must represent energy in the visible and infra red, though chiefly in the infra-red, since the G586AW glass transmits only very feebly in a small part of the extreme visible red. Since the transmission of G586AW alone was only 10.71 per cent of the total energy of the mercury lamp and since when all ultraviolet was removed the transmission was still 7.14 per cent, it is obvious that the ultraviolet transmission of G586AW could not exceed 3.5 per cent. If the absorption of infra-red by the Noviol "O" glass were taken into account, this figure would be reduced still further. When we consider that a large part of the energy from a mercury arc is in the ultraviolet and that when all this is eliminated, the G586AW filter still transmits 66 per cent as much energy as it does when the ultraviolet is present, we must conclude that the G586AW screen transmits infra-red better than it transmits ultraviolet. If then we get differences in germination under this screen it is hardly justifiable to attribute them to ultraviolet unless we have supplied our controls with an equal amount of infra-red. In any case we can hardly agree with the author that his experiments were conducted in the absence of all other radiations than ultraviolet. While it is possible that very small differences in the ultraviolet might be more effective than large differences in the infra-red we cannot be certain of this until it has been demonstrated experimentally. If, as in the case of Masure's experiments, the differences are so slight as to require statistical manipulation to bring them out, we can reasonably doubt that the ultraviolet was very effective.

It might further be mentioned that some of the significant figures are based on averages of seedlings which received exposures ranging from 15 minutes to 72 hours. This is not a very satisfactory lumping of data. In other cases individual series were analyzed. One would expect that if the ultraviolet is the effective agent in producing beneficial results there would be some relation between time or intensity of exposure and the effect produced. Yet no relation is apparent.

Masure's experiments were conducted with seeds in closed dishes placed at distances of 8.5, 17.5, and 18 cm. from the mercury arc lamp. It is difficult to understand how a fan alone would prevent heating effects from the lamp at such short distances, especially under periods of irradi-

ation lasting several hours. In his lots H and K the seeds, in Petri dishes, were covered with G586AW glass and then brought to a distance of 8.5 cm. from the arc. Under these conditions heating effects must have been pronounced.

In view of all these considerations, we are far from convinced of the validity of the author's conclusion that "ultraviolet radiation of 3650 Ångstrom units wave length, in the time and intensity employed and in the absence of all other radiations throughout the experiment, exerts a stimulative action on the subsequent rate of growth of the hypocotyl of pea seeds irradiated in the air-dry state."

Since 1927 there have also been those who have reported harmful or indifferent effects of ultraviolet on seeds and seedlings. Unscreened arc experiments in general have yielded such results and have failed to show beneficial effects.

Popp and Brown (109, 110, 111) have over a period of years carried out experiments on seed germination and early growth of seedlings using chiefly turnip and also radish, cucumber, pigweed and curled dock. These were reported in part at the New York meeting of the Botanical Society (110). Over 12,000 seeds have been used in these experiments. No less than 50 seeds per culture were ever used in any test. Fifteen different series of experiments have been completed. The seeds were usually germinated on moist filter paper and cotton and kept, except for short daily exposures to the mercury vapor arc, some in the dark, some in diffused light, and some in diffused light minus all ultraviolet. Irradiations were given with the unscreened arc and with the arc screened with various Corning filters including Noviol "O" which excludes practically all ultraviolet, G586A, which absorbs practically all visible and transmits the ultraviolet region between 320 and 400 mμ., Corex, which excludes ultraviolet below 270 mμ., and window glass which excludes ultraviolet below 313 mμ. In addition, some cultures were exposed to the ozone only of the lamp. The irradiations were usually given for ten days when rapidly germinating seeds were used. A special effort was made to provide adequate controls.

The outstanding results of these experiments have been (1) the marked and invariably injurious effect on seedlings of the radiation of the unscreened arc even for exposures as brief as one-half minute per day, (2) the lessened injurious effect of the radiation through a Corex filter, and (3) the failure of any region of the ultraviolet studied to influence significantly the rate or the percentage of germination or to stimulate the growth of seedlings. It should be emphasized that *no significant stimulation was ever obtained when adequate controls were used.* The effects were recorded by general appearance of cultures, hypocotyl lengths, leaf measurements, and dry weights.

Cluzet and Kofman (26) irradiated dry barley grains with a mercury vapor arc in quartz at a distance of 60 cm. for from 3 to 4 hours with no effect on the later development of the seedlings. Germinating seeds, however, irradiated from 3 to 5 minutes every two days showed after the first day of such treatment a discoloration of leaves followed soon by retardation of stem growth. In no case was any acceleration of growth noted. To determine whether there exists an antagonistic action between x-rays and ultraviolet rays seedlings were submitted to ultraviolet rays, the germinating seeds of which had formerly received feeble doses of x-rays. Not only did the ultraviolet not prevent the harmful action of x-rays but it accentuated it, adding its harmful effects to those of the still shorter x-rays.

Mezzadroli and Vareton (94) have reported harmful results of the unscreened arc with exposures of one minute or more at distances of 50 cm. or less, the injury increasing with decreasing wave length and increased length of exposure to the point of death. The data reported on hypocotyl lengths, however, are not very convincing one way or another except that a much smaller number of seedlings was averaged in the unscreened arc cultures. These authors also report (93) injurious effects of the region 330 to 390 mμ. if exposures are made at short distances, but no data from such irradiation are presented.

Pires de Lima (104) reports unfavorable results from the irradiation of dry rye seeds, seeds soaked in water, and seeds soaked in eosin solution exposed to a mercury arc at 30 to 80 cm. for single periods of 5 to 30 minutes and observed for one month afterward.

Tincker (156) found no differences in the rate of germination of certain vegetable seeds in frames with ordinary glass, vita glass and another ultraviolet transmitting glass. Whether the seeds were covered with soil was not stated.

Detwiler (38) reported that the exposure of dry seeds of *Ribes rotundifolium* to ultraviolet of 270 to 320 mμ. delayed germination and caused pronounced stunting of seedlings. The duration of the injury, after irradiations were discontinued, was proportional to the length of the treatment.

Viewing collectively the experiments thus far carried out on the effect of ultraviolet radiation on seed germination and the early growth of seedlings, we observe that the only fact clearly demonstrated is the injurious effect of short-wave radiation, that below 290 mμ. While there is some indication that certain ranges of ultraviolet might be beneficial in one way or another, the results so far reported are far from conclusive, and the evidence from more carefully controlled experiments would indicate little or no effect of the longer wave-lengths, those from 290 to 400 mμ.

PART II

GENERAL AND SPECIFIC EFFECTS OF ULTRAVIOLET RADIATION UPON MORE MATURE PLANTS

In the preceding paragraphs we have considered investigations dealing only with the effects of ultraviolet radiation upon seed germination and the first stages of seedling growth. Investigations dealing with effects on plants in more advanced stages of growth and on plants under observation for considerable periods of time will now be reviewed.

Experiments of this nature have been carried out in various ways. In some, the effects of single exposures or several exposures to a mercury vapor arc have been noted. In others, plants have been grown for considerable periods in daylight from which all ultraviolet rays have been eliminated by appropriate screens. In others, plants have been grown for a number of weeks under ordinary greenhouse conditions with additional short daily irradiations from a mercury arc in quartz either unscreened or covered with one of several filters. In others, artificial illumination only has been used, in combination with various filters. In still others plants grown in houses, frames or boxes with ordinary glass panes have been compared with plants under similar conditions except that the ordinary glass panes were replaced by one of a number of special ultraviolet transmitting glasses.

The results of the various experimental procedures have been recorded in a number of ways. The criteria most often used were general appearance of the plant, evidence of necrosis, height of plant, number and size of leaves, time and amount of flowering and fruiting, fresh weight, dry weight, and ash content. In addition, stem diameter, pigment development, development of spines, hairs, etc., anatomical features, chemical composition, enzyme development, and various other criteria have been used.

The discussion of the reports falling into this group is subdivided into investigations dealing with:

1. Injurious effects of short-wave ultraviolet radiation.
2. Plants grown in daylight from which the ultraviolet portion was removed.
3. Plants grown in daylight with additional short daily irradiation from a mercury vapor lamp.
4. Plants grown exclusively under artificial illumination.
5. Plants grown under special ultraviolet transmitting glasses.

Investigations dealing principally with injurious effects of short-wave ultraviolet radiation

Earlier works such as those of Siemens (146), Déhérain (35), Bailey (9, 10, 11), Bonnier (17), and Rowlee (121) with electric arc light will be

passed over. The works of Hertel (64, 65), Maquenne and Demoussy (82), Kluyver (71, 72), Stoklasa (150, 151, 153), and Ursprung and Blum (165) appeared a little later. These investigators all noted the superficial destructive action of the short-wave ultraviolet. Kluyver (73) emphasized for the first time that the destructive rays were not present to any appreciable extent in solar radiation.

More recently Arthur and Newell (8) have performed experiments to determine what region of the ultraviolet is most injurious and whether that region near wave length 290 mμ., the extreme limit for solar radiation, is injurious to plant tissue. Using a quartz mercury arc and a series of Corning filters which absorbed progressive increments of the extreme ultraviolet radiation between wave lengths 200 and 290 mμ., they noted the time necessary to produce marked injury on young tomato plants. Spectrograms and transmission curves, after continued use of the filters, were given so that the nature and amount of ultraviolet actually reaching the plants were definitely known. In addition, the total radiant energy reaching the plants through the various screens was measured by a Weather Bureau type pyrheliometer. Not more than 6 per cent variation was found to occur. Provisions were made for maintaining the constancy of the radiation of the mercury arc. The filters used were found not to solarize. Hence these experiments were performed under carefully controlled and relatively definitely known conditions of radiation.

The results showed that the time of exposure to the arc necessary to cause marked injury increased rapidly as more and more of the extreme ultraviolet component was cut off from the plants. By means of a quartz concentrating lens which increased the intensity three-fold it was also shown that apparently the time of exposure necessary to cause marked injury with a given quality of radiation is approximately inversely proportional to the incident energy. The injury produced was found not to be cumulative. That is, a plant but slightly injured by a single irradiation of a given duration through a certain filter received little further injury when irradiated through that same filter each day for several weeks for that same length of time. However, since new tissue is continually forming as the plant grows, the total injurious effect produced on a plant was much greater when it was exposed often than otherwise. No marked beneficial effects were observed in any of these experiments. Nor was any injury produced within the extreme limits of wave-lengths present in solar radiation except under conditions which never occur in nature, namely, irradiation through a concentrating lens and a screen transmitting faintly to 289 mμ. for 16½ hours. Injury did result, however, from wave-lengths but slightly shorter than those occurring in solar radiation.

These results indicate that the so-called incremental method of exposure used by Eltinge (43) and Fuller (49) is of no significance as regards its allowing the plant to become accustomed to radiation. Fuller has theorized rather elaborately on the possible benefits of such a plan, although it apparently proved successful only in a preliminary experiment of his and not in his principal experiment. Results of experiments by the authors of this review (111) also indicate that the incremental method is no different in its effect from one in which equal daily exposures are given as far as accustoming the plant to radiation is concerned. Each irradiation is effective independently of all others.

These results also indicate the incorrectness of Fuller's conclusions in his last brief experiment on infra-red radiation (50) in which he states that the infra-red is responsible in considerable degree for mercury arc injury. This will be pointed out in more detail later.

Finally, these carefully conducted experiments confirm once again and more accurately than previous experiments had, the results of earlier workers who have obtained injurious effects with short-wave ultraviolet radiation.

Investigations dealing with plants grown in daylight from which the ultraviolet portion was removed

Schanz (128) concluded that the elimination of the ultraviolet was beneficial to plants and recommended Euphos glass, which excludes ultraviolet, for greenhouses. His failure to take into consideration light intensity differences makes it doubtful whether his results were really quality effects.

Popp (108) in 1925 conducted experiments at the Boyce Thompson Institute. Here for the first time seed plants were grown in light of various ranges of wave-lengths under controlled and stated conditions, particularly with regard to light intensity and quality. When only the ultraviolet portion of solar radiation was removed by a Noviol "O" screen of the Corning Glass Works, no significant effects were produced on plants as evidenced by general appearance, development of pigments, rate of growth, time and amount of flowering and fruiting, fresh and dry weights, amount of total carbohydrates, starch content, total and soluble nitrogen, and some of the higher organic compounds. Any indications given were in favor of the elimination of the ultraviolet. If, however, the blue end of the visible spectrum was removed with the ultraviolet, then decidedly abnormal plants resulted.

The experiments of Shirley (143) have indicated that the blue violet end of the solar spectrum is more efficient in dry weight production than

the red end, when light intensities are uniformly 10 per cent of that outside. The removal of the ultraviolet and some violet, however, caused no very significant decrease in efficiency, which is to be expected when we consider the small percentage of total radiation in this region.

Jacobi (68) attempted to determine whether the formative effects of ultraviolet radiation such as dwarfing, hairiness, thicker and smaller leaves, brighter colored flowers, etc. claimed by Schanz (127) were really ultraviolet effects or whether they were light intensity effects. He grew plants under Uviol, an ultraviolet transmitting glass, and Euphos, an ultraviolet absorbing glass, under solar radiation, and then sought to confirm his results as quality effects by performing laboratory experiments with artificial illumination in which an attempt was made to equalize intensities. He concluded with Schanz that the dwarfing effects were quality effects caused by ultraviolet radiation. He went still further and determined fresh and dry weights of his laboratory plants. Fresh weights came out in favor of Euphos glass, and dry weights in favor of Uviol glass, which was thought to be an indication that ultraviolet favors dry weight production. However, the fact that fresh weights came out in favor of the Euphos glass, is an indication that one might justly be suspicious that intensity differences in radiation were in operation. There are no figures given of the actual intensities reaching the experimental plants in that part where the attempt was made to equalize intensities. It might be noted that Senn (133) has attributed dwarfing in alpine regions to greater light intensity there, but he gave quality no consideration.

The experiments seem to indicate that at low altitudes the elimination of solar ultraviolet alone has relatively slight if any influence on the plant. At higher altitudes where solar ultraviolet is more intense or under artificial radiation rich in that portion of ultraviolet present in sunlight there are indications of possible formative effects of ultraviolet, although these have not been clearly separated from intensity effects in the visible, particularly in the blue violet region. Shaw (134) and later Popp (108) have emphasized the significance of the blue end in relation to configuration of the plant.

Simon (147) in a recent semi-popular account of the nutrition of cultivated plants mentions incidentally an experiment of his with Euphos glass of the type used by Schanz. Cultures of garden plants under this glass were said to give, under otherwise similar conditions of environment and nutritional conditions, increased yields up to 50 per cent over plants grown under ordinary glass. The author, however, gives the impression that he was of the opinion that Euphos glass transmits ultraviolet better than ordinary glass does. If it was, as stated by the author, the same glass as

was used by Schanz, it *eliminated* the ultraviolet. An accurate statement of the conditions of the experiment is not given. In view of the many claims made recently for ultraviolet we wonder whether the author's results would have been as striking had he known the real transmission of this Euphos glass.

Investigations dealing with plants grown in daylight with additional short daily irradiation from a mercury vapor lamp

A glance at Tsuji's short preliminary paper in the Louisiana Planter (162) would convince any critical observer of the inconclusiveness of his extravagant claims. We mention the paper here merely because it has been referred to in later reports.

Delf, Ritson, and Westbrook (37) in 1927 attempted one of the first studies of the effects of short daily exposures of plants to the radiation of an unscreened mercury arc. Young plants of *Arachis*, *Voandezia*, and *Trifolium* exposed at various distances for short periods up to ten minutes per day were stunted, the epidermis of the leaves collapsed, and leaf mesophyll was less differentiated and more compact than in the controls. All of the irradiated plants died after the conclusion of the experiment. Of ten controls left, five were irradiated for one month for 30 seconds per day at a distance of eight feet. Two months later the irradiated plants were larger and more vigorous than the controls. As there were just five of these plants, the results were considered only "suggestive." They were never repeated. Harmful effects were obtained in various other experiments and were more marked on plants given shorter daylight illumination per day than on those given longer periods in the light.

Eltinge (43) has set down observations on rooted cuttings and young seedlings of plants grown for a number of weeks under ordinary greenhouse conditions with additional daily irradiations from a mercury vapor lamp at distances of 50 and 100 inches. Plants were exposed to the unscreened lamp, to the lamp covered by vita glass which was said to transmit down to 289 mμ., or to the lamp screened by quartzlite glass which was said to transmit down to 313 mμ. The irradiations were given by the incremental method, that is, for a period of one half minute the first day and for periods increasing by one half minute each day, on succeeding days.

While a considerable total number of plants was used, there were too many different species under too many different conditions so that generally no more than six to ten individuals of a given species were given a similar treatment. Average figures recorded in tables, therefore, are computed from data on six to ten plants grown under variable environmental conditions for from four to eight weeks. While all of her beneficial results

were attributed to ultraviolet radiation, she had no controls to eliminate the possibility of visible, infra-red, temperature and other effects of the lamp, since her so-called controls received no irradiation whatsoever from the lamp. Furthermore she made no measurement of the quality or intensity of ultraviolet reaching her plants under the various conditions used.

The only consistent result of treatments was injury by the unscreened arc to all plants used. Individual groups of plants irradiated through vita glass or quartzlite glass did prove superior to non-irradiated plants in a number of cases, but the differences were often slight and no one type of glass gave uniformly better results. The superiority expressed itself differently in almost every set of plants in which it appeared. It might be greater height, greater thickness of stem, larger leaves, greater number of leaves, greater average rate of growth, greater rate of growth during the last days or during the last weeks of the experiment, earlier flowering, or better color of plant. There were various combinations of these features. The same treatment caused stimulation in one respect and retardation in another. For instance, no type of irradiation proved superior to controls for *Raphanus* and *Nicotiana*. For *Bryophyllum* and *Phaseolus*, vita glass and a distance of 50 inches from the lamp proved best. For *Coleus*, vita glass and 100 inches was best. For *Zea Mays*, vita glass and a distance of 100 inches, and quartzlite glass and 50 inches distance from the lamp gave equally superior results. For *Lactuca*, quartzlite glass and 50 inches distance from the lamp caused the most leaves to develop, but they were smaller than those of controls. Cultures under vita glass at 50 or 100 inches had fewer leaves than those under quartzlite at 50 inches, but more and slightly larger leaves than control cultures. For *Cucumis*, vita glass and 50 inches distance proved superior for stem elongation, but the control plants had more leaves. For *Ipomoea* quartzlite and 100 inches distance proved best for stem growth, but quartzlite and 50 inches were equally as good as quartzlite and 100 inches for leaf number, and both were better than controls. To illustrate the effect of the same irradiation treatment on three different sets of plants, the results of irradiation through vita glass at a distance of 50 inches may be cited. For *Zea Mays* at first the control plants grew taller, but during the last few days the rayed plants grew very rapidly and surpassed the controls. Rayed stalks were larger in diameter, rayed leaves outnumbered control leaves and were larger. For *Nicotiana*, however, the observations pointed toward a retardation of growth, though there was no evidence of burning. For *Ipomoea*, little difference was noted between rayed and control plants although the rayed plants had more leaves.

Such results point far more likely to differences resulting from inherent

variations of the plants themselves coupled with environmental variations of one type or another not taken into account. Certainly we should hesitate to attribute such varied effects solely to one variable under the conditions used in her experiments. Miss Eltinge's conclusion that "each plant has its own ultraviolet requirement for best growth which can be determined only by experiment" rests upon the assumption that the ultraviolet was the only variable in the test plants as compared with the controls. This obviously was not the case.

From the Michigan Agricultural Experiment Station (2) comes the report that four minute daily exposures of soybeans and tomatoes to ultraviolet radiation down to 200 mμ. at a distance of one meter from a mercury vapor lamp caused injury in every case. The conclusion that a daily treatment of one minute at 9 A.M. increased the dry weight 10 per cent while a similar treatment at 3 P.M. resulted in a 7 per cent decrease is difficult to comprehend. Unfortunately this is just a progress report and no data are given which would enable one to interpret the effects reported.

Hey and Carter (66) tested the effect of the Hanovia Artificial Alpine Sun Lamp at 48 inches for periods of one and three minutes daily on the vegetative growth of wheat seedlings and their infection by *Erisiphe graminis*. They report no stimulation of growth for the variety "Little Joss," but uniformly taller and stronger plants in one experiment with the "Persian Black" variety. This, however, was not verified in a second experiment in which no stimulation was evident. A three minute daily exposure greatly reduced infection by mildew on the susceptible variety "Little Joss." When the treatments ceased, the plants again became infected. The authors attribute suppression of fungus growth in wheat fields in hot dry summers to the increased amount of ultraviolet present in solar radiation and its increased growth in wet weather to the decreased amount of ultraviolet present. One of the serious errors in this generalization is that solar ultraviolet is different in quality and intensity from that of the artificial source used.

To date Fuller has published four times. The first report (48) was a brief summary in "Science" of work which was later reported more fully in the "Annals of the Missouri Botanical Garden" (49). The third, with Wynd as co-author (173) was a brief report on analyses of the ash of some of the plants used in one of the earlier experiments. The fourth (50) was a note on the effects of infra-red as compared with ultraviolet effects of a mercury vapor lamp. His work has been with young tomato and cucumber plants.

The first three reports are based upon one preliminary and one major experiment in which untreated plants in a greenhouse were compared for

several weeks with plants given daily irradiations from a mercury vapor lamp either unscreened, screened with vita glass, or screened with quartzlite glass. The daily periods of irradiation were either constant for 7.5 or 9 minutes per day or incremental, starting with one half minute per day and increasing by one half minute each succeeding day. The similarity to Eltinge's procedure is evident.

In the first experiment only 15 plants per treatment were used. In the second and principal experiment 100 plants per treatment were used. The injurious effects of the unscreened arc were again noted. In addition, stimulation of plants by ultraviolet radiation is claimed as evidenced by increased height, number of leaves, fresh weight, dry weight, ash weight, and calcium content, over controls. Tests on phosphorus content were also made, but no increase was noted in irradiated plants. Although the author states in his summary that "statistical analyses proved the reliability of the results" of his major experiment he has not statistically analyzed plants which varied in treatment only in the quality of ultraviolet radiation received, and therefore his statistical analyses are not significant as indicating ultraviolet effects.

The "controls," as far as can be gathered from the data, were kept constantly in the greenhouse. The test plants were irradiated daily with a mercury vapor lamp. In these irradiations the plants received not only additional ultraviolet radiation not received by the controls but also additional visible and infra-red radiation as well as ozone. Moreover, the plants irradiated under vita glass and under quartzlite glass were under conditions which differed not only in the quality of ultraviolet present as was assumed, but also in the total intensity of ultraviolet present, and in the quality and intensity of visible and infra-red. Furthermore no attempt was made to record differences in intensity of radiation received by the plants compared except for total radiation intensities under the various conditions. Yet the author assumed that the one variable in his experiment was quality of ultraviolet, made his statistical analyses and drew his conclusions on this false assumption. This is strange in view of the fact that he has stated in the introduction of his principal paper (49) that "it is a flagrant disregarding of facts to assume that the effects of the mercury arc on organisms are due to the ultraviolet region alone."

Examination of data as recorded gives additional reason for questioning the validity of the conclusions. It is difficult to understand why the author concludes regarding the method of irradiation that "the incremental method for the most part produces greater growth than the constant period method, indicating an induced adjustment of the plants to the gradual increase of dosage" when, in the principal experiment only six tests out

of sixteen on height, number of leaves, fresh weight, and dry weight indicated better results for the incremental method as compared with the constant period method, and when his most outstanding favorable effects were obtained with plants irradiated by the constant period method. Previous work (8) has demonstrated that if, for example, one dose of ten minutes is injurious, previous exposures of the plant to smaller doses will not prevent injury by a ten minute dose later. We have tested out this method in our own laboratory and have obtained no better results by the use of the incremental method.

The only very outstanding experimental result reported in the first three papers is the better growth of plants under vita glass given constant daily exposures of nine minutes per day as indicated by height, number of leaves, and fresh weight. For tomatoes the dry weight percentages of fresh weights also were greatest under these conditions. For cucumbers, however, the dry weight percentages of the vita glass constantly exposed plants were less than those for both vita glass and quartzlite glass incrementally exposed plants by 0.1 per cent and 0.03 per cent respectively. These are not very great differences. The other results show fluctuations in no very consistent manner, the plants being in no great degree different from each other. It appears doubtful whether the irradiation treatments alone influenced the variations. In the principal one of these three experiments four sets of 100 plants each of cucumbers and tomatoes were irradiated at 100 inches from the mercury vapor lamp, two through quartzlite screens and two through vita glass screens. One set under each screen was irradiated for nine minutes daily and the other for one half minute the first day and a period increasing by one half minute each succeeding day. Through quartzlite glass the constant method of exposure gave the best stem growth in tomatoes, but the control plants and the incrementally exposed plants proved superior to the constant period plants for cucumbers. The control cucumber and tomato plants had more leaves than those exposed by the constant method, but fewer than those exposed by the incremental method. Fresh and dry weight percentages of irradiated plants in all experiments were greater than those of the control plant weights; but cucumbers gave the greatest fresh and dry weights by the incremental method while with tomatoes the constant period method proved superior. No ash analyses were made of these plants. If the vita glass incremental cultures are brought into the comparison the cucumber cultures proved inferior to all other cultures including controls in height, inferior to all other cultures except quartzlite constant period cultures in number of leaves, superior to all others except vita glass constant period cultures in fresh weight and superior to all others in dry weight. Tomatoes incrementally exposed under

vita glass, on the other hand were better than controls, about equal to quartzlite incrementally exposed plants, and inferior to other plants in height, superior to all except vita glass constant period plants in number of leaves and in dry weight, but exceeded by quartzlite and vita glass constantly exposed plants in fresh weight. Such variation within small limits offers no very convincing proof of beneficial effects of ultraviolet radiation. Whether the irradiation was the cause of the greater size of the plants in the vita glass cultures under the constant period method was never checked by a repetition of the experiment. Certainly that the ultraviolet portion of the irradiation was the determining factor was in no way proved because of lack of adequate control plants and lack of accurate measurements of the radiation reaching the plants. Since the ash analyses for calcium and phosphorus content were made with some of the control and vita glass constantly exposed plants of the experiments just referred to, the same criticisms hold true for the results given in this paper as in the one above, namely, that comparisons were not made between plants which differed in treatment only in the quality of ultraviolet received.

In the fourth paper Fuller concludes from an experiment with twelve tomato plants per culture, with three cultures that the injurious effects of the open arc at short distances are due in considerable degree to infrared radiation from the arc. Here again the author has worked with relatively uncontrolled conditions with regard to the radiations under consideration. He assumes that interposing a 1.5 cm. quartz water cell between the mercury arc and the plants caused no diminution in the intensity of the ultraviolet reaching the plants as compared with the unscreened lamp. That this is not true is indicated by an examination of the coefficients of absorption of water in the ultraviolet as given in the International Critical Tables. In addition, measurements made in our laboratories with a Westinghouse P.E. Ultraviolet Meter indicate that the ultraviolet intensity is cut down 25 per cent in passing through such a cell. Furthermore, the shorter the wave-lengths the greater is the absorption. Thus the destructive radiation is reduced much more than the longer, less destructive radiation. Obviously the diminished injury by irradiation through the water cell cannot be assumed to be due merely to the elimination of infrared.

Furthermore, a number of investigators have demonstrated that the more the short waves of the open arc are cut off from plants by appropriate screens, the less injury is there to the plants. Arthur and Newell (8) under very carefully controlled and measured conditions of radiation have shown this. They, as mentioned previously, used filters which absorbed progressive increments of the extreme ultraviolet component from the lamp to-

ward wave-length 290 mμ. The time of exposure necessary to cause injury increased rapidly as more and more of the extreme ultraviolet was absorbed by the filters, yet the difference in total transmission through the various filters, including the infra-red transmission, was very slight, varying no more than 6 per cent. The possible injurious effect of infra-red radiation of high intensity is by no means denied, but Fuller's experiments do in no way indicate that the injurious effects indicated for short-wave ultraviolet by the more accurately controlled experiments of previous investigators are without foundation. If Fuller actually wished to demonstrate injurious effects of infra-red it is difficult to understand why he did not expose some plants to the infra-red in the absence of all ultraviolet.

Popp and Brown (111) in addition to previously reported experiments have carried out five series with buckwheat. In two of these, 2-minute daily exposures to radiations from a mercury arc were given for ten days; in the other two, half hour daily irradiations were given. In one 2-minute series and one half-hour series the seeds were planted in soil and the first irradiation given when the seedlings were several inches high. In the other two series the seeds were placed on moist filter paper and cotton and irradiated for the first time three days later, that is, after the seeds were well germinated. Fifty seeds per culture were used. Exposures were given to the open arc, to the arc screened by Corex glass, by window glass, by Noviol "O" glass and by G586A glass. In addition one culture was kept in diffused light with no irradiation, and one was exposed to the ozone only of the lamp. No favorable effects of the ultraviolet used in these experiments were obtained. The injurious effect of the unscreened arc was again manifested.

Investigations dealing with plants grown exclusively under artificial illumination

Withrow and Benedict's experiment (170) was unique in that they grew tomato and *Coleus* plants from seed for a period of three months under artificial illumination as transmitted by various cellophane filters. Theirs was an attempt to determine whether the region 290 to 313mμ., that region said to be of such importance to animal life, was essential for optimum conditions of plant growth. They state that others have failed to obtain stimulation either because they did not have present a sufficient intensity of the rays 290 to 313 mμ., if daylight was the source of radiation, or that in addition to a sufficient intensity of the rays 290 to 313 mμ. there were also present some of the shorter lethal rays, if the mercury arc was the source of radiation. In the use of artificial radiation they have a controlled light source with considerable intensity in the ultraviolet region.

They used cellophane filters especially developed for the experiment (169) the transmission curves of which showed sharp cut-offs at the desired wave-lengths, a quality said not to be possessed by many glass filters which have been used. Their results indicated to them that "the removal of the 2900–3100 Å. ultra-violet region is detrimental to the growth of tomato and *Coleus* plants, and that the inclusion of a small amount of lethal radiation of shorter wave length than 2900 Å. is sufficient to mask the beneficial effect of the 2900–3100 Å. region." This was indicated by the greater height and growth rate, greater internodal length, greater stem diameter, greater number and average area of leaves, and greater fresh and dry weights of those plants which received radiation in the region 290 to 310 mμ., with no shorter ultraviolet present. The final statement in the paper, however, reads that "because of the limited number of plants used and the inadequate growth conditions, especially with regard to intensity of illumination, these results are offered simply as preliminary data, indicating the possible growth-promoting action of the 2900–3100 Å. ultra-violet region."

Unfortunately the total light intensity was only about 30 foot-candles, an intensity so weak that it resulted in etiolation of the plants. None of the plants, therefore, was normal, except the so-called controls which were kept in the diffused light of a window sill with a southern exposure. These "controls" were not used in any of the measurements, and justly so since they were under conditions totally different from those of all other plants. While the cellophane filters used in this experiment were said to be stable, they were also said to show slow deterioration under intense irradiation. No further indication is given of the degree of stability of the filters. No measurements of total energy under the various screens are given. Such measurements would have been of particular value since the illumination intensity was probably below the minimum for normal growth and hence small differences in the different compartments might have caused pronounced effects on the plants.

The data recorded represent for tomato comparisons of measurements on 2, 6, and 14 plants respectively, and the fourteen plants under supposedly identical conditions show average measurements per pot to be more variable than average measurements of plants under different conditions. The tomato data are obviously of little value. The *Coleus* data were obtained by picking out three "representative" plants from each of five pots of ***indefinite numbers of unthinned plants*** under each condition. The photographs of these plants show decided crowding in the pots which is very unfortunate particularly when the illumination intensity was extremely low. It is difficult to understand why so many plants were used

per pot and on what basis any of the plants in any pot could be considered "representative." The photographs show that in any pot there was extremely wide variation in size of plants. Such data also are of limited value. There was no repetition of any of this work. While there is a possibility in these experiments of the favorable effect of the region 290 to 310 mμ., the conditions under which the experiments were conducted were such as to offer very legitimate reason for doubt of the conclusions arrived at.

Investigations dealing with plants grown under special ultraviolet transmitting glasses

Since the region 290 to 313 mμ., that region of the solar ultraviolet which is not transmitted by ordinary window glass, has been emphasized as necessary for the normal development and health of higher animals, a series of special ultraviolet transmitting glasses has been developed and put on the market. Various Corning glasses of this country and vita glass of England are among these. There are also numerous German glasses known by various trade names such as Uviol glass of Schott and Genassen, Jena; U-glass of Dresden, Ultraviolet glass of Berlin, Ufau, Ultra, Brephos, Ultravit, Sendlinger, Bios, and Sanalux glasses. Probably the Jena glassworks of Germany antedates all others in manufacturing ultraviolet transmitting glasses, having made them as early as 1903. Their Uviol glass in comparison with five other German glasses was found to transmit further down in the spectrum than any of the others and to transmit a higher percentage throughout in the ultraviolet than any of the others.

These new glasses differ from each other considerably in ultraviolet transmission and in addition some of them solarize, that is, lose a part of their transmission in the ultraviolet upon exposure to light (8, 44, 171, 172). This solarization is far more marked when the glass is used under a mercury arc than when used in ordinary sunlight. In a few cases glass substitutes have been tried, but these usually have not been found as satisfactory as glass screens (8) (169, 29). It is obvious that when one of these screens is used, the actual quality and intensity of the ultraviolet reaching the plants is questionable unless definite measurements are made regarding its transmission from time to time.

Unfortunately, not only is the ultraviolet transmission of these glasses different from that of ordinary glass, but so also is the visible, and in great degree the infra-red transmission. These features have been indicated by transmission curves of the glasses and by the temperature differences occurring under the two types of glasses. Any effects, therefore, obtained under one of these new glasses, cannot justifiably be said to be ultraviolet effects, but must be attributed to the difference in total transmission of

the glasses used, other environmental conditions being constant. Yet the majority of investigators who have used these new glasses have placed the emphasis on their relatively greater ultraviolet transmission.

Many of the experiments conducted with these new glasses have not been carefully controlled aside from radiation conditions so that results are correspondingly inconclusive. The fact that a small number of plants was used in many cases is also unfortunate, and failure to repeat experiments, still further reduces the value of results obtained since very often those who have repeated their experiments were unable to duplicate their original results. Most of the experiments of this type have been carried out from a practical viewpoint by greenhouse keepers, horticulturists, and floriculturists with practical results rather than scientific data as the aim and purpose.

In this country one of the carefully performed experiments of this nature was carried out at the Boyce Thompson Institute (6). Several species of flowering plants were grown under Uviol glass which transmits 80 per cent at the extreme ultraviolet of sunlight and no differences were observed in growth habit, time and amount of flowering or amount of green tissue produced as compared with plants grown under ordinary greenhouse glass. "We have yet to find any distinct advantage to the plant in growing it under a glass which transmits the extreme ultraviolet region of sunlight."

Osmun (99, 100) obtained favorable results under vita glass for lettuce and radish one year, but during the next year continued experiments gave contradictory results. The first year, radishes under vita glass showed a gain of 71 per cent in weight of the entire plant and 124 per cent in weight of roots as compared with an equal number of plants under ordinary glass. Similarly lettuce gained 76 per cent in weight and formed more compact heads under vita glass. The next year radishes averaged 10 per cent less in weight under vita glass than those under ordinary glass in one test and 14 per cent more in another. Lettuce under ordinary glass this second year weighed 3 per cent more than that under vita glass. Obviously nothing concerning ultraviolet radiation can be concluded from these results.

Tottingham and Moore (159, 160, 161) have reported on horticultural investigations at the Wisconsin Agricultural Experiment Station. In the principal paper (161) a small number of plants of twelve different species which had been under vita glass for a number of weeks was compared with plants similarly treated but grown under window glass. The comparisons involved the nature and amount of growth, dry weights, and partial chemical analyses. As stated by the authors "The present investigation is concerned with the elimination of a small portion of ultraviolet (about 3100

to 2900 Å.) in sunlight by the screening effect of common glass," but there is no mention in the summary of any favorable results under vita glass being due to the region 290 to 310 mμ. alone. Favorable results mentioned for plants grown under vita glass are ascribed rather to "the more extensive irradiation under vita glass," and there is mentioned the desirability of separating infra-red and ultraviolet effects. They recognized the high transmission of vita glass in the infra-red. At the end of the paper they state that "the present investigation is hardly more than a limited survey" and that "for conclusive results each species tested would require further examination."

Regarding the interpretation of the differences found in plants under vita glass as compared with those under common glass it is evident that the authors attach great significance to slight differences in favor of vita glass, which have been obtained with small plant populations not grown under carefully controlled conditions and often not checked by repeated experiments. For instance, corn was planted on March 30 in flats under vita and common glass respectively. One month later eight plants from each flat were weighed and showed that percentage dry weights as compared with fresh weights were 7.5 and 6.7 respectively for vita and common glass. "There was therefore a somewhat greater yield of dry tissue under Vitaglass." "Tassels and silks appeared . . . two days earlier under Vitaglass than under common glass." At this time "to promote maturation the cultures were reduced to two plants, each . . . and received an application of KNO_3." Weights on parts of the two stems from each culture (the three internodes adjacent to the best ear) revealed greater weight for those under vita glass.

The most consistent "compositional response" to vita glass was an increased percentage of lipides in the dry matter. In five out of sixteen tests the ether extracts from plants under vita glass were either lower or no higher in lipides than were those under ordinary glass. The other eleven cases showed slightly higher percentages for plants under vita glass. In another paper (159) entitled "Are Leaf Lipides Responsive to Solar Radiation" a higher percentage of lipides for tomato plants under vita glass is again reported.

While these percentages are small, the fact that increases have been reported in a number of cases may indicate a vita glass effect. Certainly, however, from such experiments we are not justified in attributing this to effects of the region 290 to 310 mμ. alone.

In England there have been numerous reports on plants grown under the English vita glass including those of Russell (122), the Kew Gardens (70), Saleeby (125), H—— (60), Colman (27), Westfield College (1),

Maddock (81), Thomson (155), Graham and Stewart (57), Tincker (156) (157), Pilkington (103), and Secrett (132). In Germany results of experiments on plants grown under the various German glasses of this type have been made by Kache and others (69), Dix (40), Herold (63), Reinhold alone and with others (116, 117, 118), Roeder (119), Grossman (59) and one anonymous (3). A detailed review of these experiments is not necessary here inasmuch as the majority of them were ordinary greenhouse experiments without adequate controls and all of a very preliminary nature. As might be expected there is no general agreement among them as to the results obtained.

In Sweden Lamprecht (76) has carried out one of the most careful investigations of this type. He has compared plants grown under Helasan glass which transmits about 50 per cent of the solar radiation from 290 to 310 mμ., a somewhat higher percentage of ultraviolet than vita glass transmits, but not as high a percentage as Uviol glass transmits. The plants were carefully handled and spaced and environmental conditions made as uniform as possible. Great care was taken to have the thickness of glass panes comparable in the test and control houses in order that the intensity of radiation reaching the plants should not vary because of this factor. Relatively large numbers of plants, never less than 40, under each condition in each test were used, and each series of experiments was repeated several times. The results were treated statistically and probable errors taken into account. Fresh weights and dry weight percentages were determined and various chemical analyses made.

Six series of carrots were run with 46 to 122 experimental plants used in each series. In no case did the use of Helasan glass result in significantly increased fresh weight, dry weight, or any change in chemical composition. One series of parsnips and one of radishes, both root crops, as were the carrots, gave similar results. Two series of lettuce plants gave no significant differences in fresh or dry weights due to the type of glass used, but indicated a definite trend in dry weights in favor of Helasan glass. Two series of spinach, also a crop with large leaves, gave results similar to those of lettuce.

The conclusion regarding the effect of the ultraviolet portion of the solar spectrum as revealed by these experiments was that there was the possibility of a certain small significance in the production of dry weight, but that definite establishment of this point could only come from much more carefully conducted experiments. For the practical horticulturist the author thought the glass to be of little value.

A review of the facts brought out by these reports in regard to evidence for ultraviolet effects by the use in greenhouses of special ultraviolet transmitting glasses reveals that out of 31 reports, unqualifiedly favorable results are reported in only 8 cases and the data for these are either not given or are of questionable value. The other articles report either conflicting results, results which could not be duplicated, very slightly favorable, or indifferent results. Of these at least 10 report the greater temperatures or heat effects under the special glasses. Several report more favorable results under them early in the spring, but not in the summer; a number report solarization effects of the glasses. The most carefully conducted experiments show nothing or very little in favor of the new glasses. Even were we to assume that all the beneficial effects reported were true, we should still have to hesitate to recommend the use of the special glasses for greenhouses because of the slight differences that have been found in even the most favorable reports.

Summary of the investigations dealing with general and specific effects of ultraviolet radiation upon more mature plants

Viewing as a whole the evidence presented in this large group of papers on the effects of ultraviolet on more mature plants, we observe that the only point which seems to be clearly demonstrated is that the short-wave ultraviolet, that from 289 to 200 mμ. is distinctly harmful. Even in very slight doses it has never satisfactorily been demonstrated to be beneficial. The degree of injury increases with decrease of wave length, increase of intensity and with greater ease of penetration. While we would not overlook the possibility of beneficial effects being demonstrated for the longer wave-lengths when accurately controlled experiments are forthcoming, the evidence from the most accurately controlled experiments to date shows little if any outstanding beneficial effect of that region of ultraviolet present in sunlight, particularly the region 291 to 313 mμ., which has been given much emphasis in animal and human physiology and has consequently been assumed by many to have beneficial effects on plants. Consequently we would not expect to find striking effects to be produced by this region in the future. It should be remembered that this region makes up a very small percentage of the total solar radiation reaching the earth. Certainly it has been demonstrated that many different kinds of plants can be grown from seed to seed in the total absence of all ultraviolet without exhibiting any very outstanding difference from plants receiving solar ultraviolet.

PART III

OTHER EFFECTS OF ULTRAVIOLET RADIATION UPON SEED PLANTS

Certain points relative to the significance of ultraviolet radiation which have not been mentioned in the preceding discussion will now be noted briefly.

The degree of penetration of ultraviolet radiation into plant cells

Of great importance with regard to the effect of ultraviolet radiation upon plants is the question of the degree of penetration of these rays into the various plant tissues, since only those rays which penetrate can be effective in producing results. Undoubtedly the facts that certain plants are more resistant than others to the harmful action of short rays, certain parts of a given plant more resistant than other parts of the same plant, and the same parts of a given plant more resistant at one stage of development than at another, owe their explanation in part at least to differences in degree of penetrability and absorption of these injurious rays. Different degrees of penetrability may also explain some of the conflicting results of past experiments. Thus the shorter lethal ultraviolet regions are ineffective if they strike plant parts opaque to them. Furthermore, any beneficial rays would have to enter the cells before they could be effective. Different media vary considerably in their capacity to transmit radiation of various wave lengths.

In earlier investigations the penetration of injurious rays only, was considered, and the degree of penetration was known only indirectly by the degree of injury produced on the plant cell as a result of irradiation. Maquenne and Demoussy (82), Kluyver (71, 72), and Ursprung and Blum (165) noted the superficial action of ultraviolet radiation of short wave lengths as indicated by the fact that only epidermal cells or those immediately beneath them were destroyed. They assumed that the harmful rays were absorbed by these external layers and failed to penetrate more deeply. Stoklasa (150) found that flowers were much more sensitive than leaves to short-wave ultraviolet, and that both leaves and flowers of hothouse plants were more sensitive than those of outdoor plants. Dangeard (32, 33) by noting various degrees of injury in different plants which had been irradiated assumed differences in degree of penetration of the harmful rays. He also thought that hairy leaves retarded penetration more than glaucous or smooth ones. Schroeter (130) thought that the thick cuticle of alpine plants protected them from the destructive action of the short wave lengths present in solar radiation. Köhler (75) using the cadmium line at 275 mμ. showed that cuticularized, suberized, and lignified walls were not

penetrated by waves of this length and explained the greater resistance of some leaves to ultraviolet on the basis of differences in the degree of penetration of the harmful rays. Schulze (131) by photomicrographs also demonstrated that the cuticle, epidermis, and xylem absorb strongly in the region of 280 mμ. while parenchyma, phloem, and young cambium are quite transparent to this region. He found strong absorption to occur in the middle lamella. He and Köhler showed that the nucleus absorbs strongly at wave-lengths 280 mμ. and 275 mμ. respectively. Dhéré and De Rogowski (39) found that pure chlorophyll was remarkably transparent to ultraviolet but that the natural chlorophylls in ether solution had a common absorption band near the middle of the ultraviolet spectrum, which would be at about wave length 304 mμ.

More recently Bucholtz (20), Metzner (92), and Shull and Lemon (144) have published on this subject. Bucholtz noted that leaves of *Mnium* and the stamen hairs of *Tradescantia reflexa* were much more resistant to the lethal action of ultraviolet than bacteria and paramoecia, probably because of the greater opaqueness of the cells of higher plants. He used wave-lengths of the range 3654 to 2378 Å.

Metzner's work (92) was rather extensive. He used long wave ultraviolet (350–400 mμ.) in his studies and his results were determined photomicrographically so that he had direct evidence of the actual penetration. He found that cellulose, hemicellulose and silicified walls were relatively transparent to this region. The plasma and nucleus absorbed weakly. On the other hand, corky and cutinized walls, and lignified ones to a lesser extent absorbed strongly in this region. Particularly strong absorption occurred in the cell sap of the epidermis, guard cells, and mesophyll of many plants; this absorption was thought to be due to the presence of tannins and flavones and to be of biological significance.

Of importance in relation to the effect of ultraviolet radiation upon seed germination is the paper by Shull and Lemon (144), which deals with the penetration of various seed coats by the radiation of an unscreened quartz mercury arc. Results were determined by spectrograms. They found that, with a maximum duration of irradiation of one hour, only the longer ultraviolet rays penetrated seed coats, the lowest limit being indicated by a feeble line at 312 mμ. and penetration of rays shorter than 363 mμ. always being feeble. There was some variability in penetration shown by different species. Even in the same seed coat there was variation. Thus in the case of corn grain membranes penetration was greatest on the embryo side. Wet coats differed little from dry ones as far as penetrability was concerned.

In this paper there is an actual demonstration of the reason mentioned

as a probability by Popp in 1921, for the failure of the short-wave ultraviolet to injure ungerminated seeds, namely, the failure of these rays to penetrate the seed coat. This paper also gives evidence which suggests that the region of ultraviolet used in Masure's investigation did actually penetrate the seed coats of his seeds.

It should be noted that no determinations of penetration to date have given percentage transmissions of various wave lengths through seed coats or any other plant parts. In other words, we have only qualitative and no quantitative data.

Effects of ultraviolet radiation upon anatomical structure

Since the penetration of the shorter ultraviolet rays is probably not very great, one would not expect them to have any considerable direct effect on the anatomical structure of plants except for the destructive action to the superficial cells. There is, of course, the possibility of chemical changes being brought about in the superficial layers which might in turn affect deeper lying cells, but we have no evidence for this. As for the longer more penetrating ultraviolet rays there is no evidence of their effectiveness in this field either.

Pfeiffer (102) reports that plants grown in daylight under Noviol "O" glass, which cuts off practically all ultraviolet, are less stocky, less sturdy, more watery, and weaker in vascular development than those grown under Corex glass which transmits all wave-lengths of solar ultraviolet.

From the fact that stem diameters, stem heights, fresh weights, dry weights, percentage of moisture and chemical analyses of plants grown under similar conditions by Popp (108) showed no marked differences we should not expect to find marked internal anatomical differences. Such differences were not found by Popp. The difficulty in obtaining sufficient and comparable material for anatomical study under such conditions renders anatomical differences found of doubtful significance unless they are very marked.

With the quartz mercury arc as a source of radiation Delf, Ritson, and Westbrook (37) have recorded as unscreened arc effects on leaves, in addition to the collapse and death of the epidermal cells, a decrease in thickness of the leaf, more compact mesophyll and palisade tissue and a reduction of mechanical tissue. Eltinge (43) in general has duplicated these results. Her anatomical data on plants screened either by vita glass or quartzlite glass indicate no outstanding effects for any given treatment.

Dane (30) has described unscreened arc effects on soybean stems. Irradiated plants had stem diameters one and one half times as large as the stems of controls. There was a reduction in the number of medullary rays.

Meristematic tissues remained active for a longer time in irradiated plants than in the controls. While the cells of the medullary rays under ordinary conditions remained parenchymatous, in irradiated plants they developed into xylem and phloem. Irradiated stems became hollow.

None of these experiments with artificial radiation were carefully enough controlled to warrant ascribing the effects noted for irradiated plants to ultraviolet alone.

The effect of ultraviolet radiation alone on anatomical structure is still largely to be determined.

The relation of ultraviolet radiation to the formation of chlorophyll and anthocyanin

While Stoklasa (150, 151) noted that exposures not exceeding two hours to wave lengths 300 to 500 mμ. of a mercury arc generally caused a rapid development of chlorophyll in etiolated plants, and that etiolated plants exposed to this region of sunlight became green more rapidly than those exposed to full sunlight, Dangeard (31) claimed that blue and violet light from a Nernst lamp seemed to have little influence on chlorophyll synthesis, and that the energy absorbed below 490 mμ. was insufficient to bring it about. Sayre (126) has said that with sufficient energy value chlorophyll develops in that region of the ultraviolet between 300 and 400 mμ. In many reports a deeper green color of plants under one of the special ultraviolet transmitting glasses has been reported, but it should be noted that this is not necessarily an indication of greater chlorophyll development, as this appearance may be brought about by a more compact tissue, a broken down epidermal layer, lack of hairiness, etc. In addition, as has been indicated before, effects under these special glasses are not necessarily ultraviolet effects. Colla (28) found that chlorophyll developed in plants exposed to radiation of wave-lengths 330–390 mμ. the amount being comparable to that produced in ordinary light of low intensity. In none of these cases has there been quantitative determination of chlorophyll.

Shirley (143) determined quantitatively the amount of chlorophyll developed using the method of Willstätter and Stoll as modified by Shertz. Plants grown under a blue glass transmitting the region between 374 and 585 mμ. under 10 per cent of the total intensity of daylight often gave a higher concentration of chlorophyll than any other light qualities used under the same intensity. At the same time the chlorophyll concentration was usually lower under G34 glass which transmits no radiations shorter than 529 mμ. He found that "in all light qualities used the plants increased their chlorophyll concentration with decreasing intensity to a certain point." When plants from which only the ultraviolet was removed under

65 per cent of the total intensity, were compared with those receiving the full spectrum of daylight under 68 per cent intensity, no significant difference in chlorophyll content was found in *Geum*, sunflower, or *Galinsoga*. This is the only investigation in which quantitative determinations of chlorophyll were made under various light qualities.

A relationship between ultraviolet radiation and the development or presence of anthocyanin and related compounds in plant cells has been suggested in a number of cases. Shibata, Nagai and Kishida (139, 140, 141, 142) found that the cell sap of epidermal and peripheral parenchymatous cells of the aerial parts of plants in general, commonly contained flavone derivatives. Furthermore, according to them, these compounds were limited almost exclusively to these parts of plants. They also noted that plants in sunny habitats contained greater amounts of flavones than those in shady places, and that alpine plants were richer in flavones than those in lower regions where the intensity of solar radiation was not as great as in alpine regions. In general plants exposed to intense sunlight showed a greater development of flavones than those under lower intensities unless the plants were protected by some morphological feature such as a thick cuticle. Thus *Ficus elastica*, a tropical plant grown under strong light intensity had leaves with a low amount of flavones, but these leaves had a thick cuticle. Rosenheim (120) thought that if the findings of Shibata, Nagai and Kishida were true, then alpine plants grown at lower altitudes should not contain as much flavone as those grown in alpine regions. Using *Edelweiss* as an example he found that this plant actually did not develop as much flavone when grown at lower altitudes as when grown in the Alps.

Schanz (128) noted that much of the red color of red-leaved lettuce grown outdoors disappeared when the plants were placed under ordinary window glass which cut off most of the radiation below 320 mμ., while all of it disappeared if wave lengths shorter than 388 mμ. were eliminated. When young plants of *Celosia Thompsoni* with dark red leaves were placed in daylight under various screens the new leaves which formed were less red and more green the more the short wave lengths were eliminated, and were completely green when wave lengths shorter than 420 mμ. were removed. Red beet leaves lost the red color in the absence of ultraviolet radiation, but the stems and petioles remained red.

These investigators have all attributed possible biological significance to the development and presence of these anthocyanins and flavones. One of the possible rôles suggested for these substances was that they absorb ultraviolet radiation and consequently protect deeper lying cells from its injurious effects. Metzner (92) has demonstrated that strong absorption of the region 350 to 400 mμ. occurs in cell sap which contains tannins and

flavones. However, this hypothesis loses weight when it is remembered that ultraviolet radiation of the intensity and quality present in solar radiation has never been conclusively demonstrated to be injurious to plants. Such evidence as is available, as for example that of Arthur and Newell (8), indicates rather that ultraviolet of the intensity and quality present in daylight is not injurious.

One of the possible demonstrations of the injurious effects of solar ultraviolet is indicated by Schanz's experiment with the purple beech (128). While the experiment was not carried out with proper controls it does indicate a possible destructive action of short wave radiation on plants containing epidermal anthocyanin when they are first grown under conditions which prevent the development of this anthocyanin and later exposed to radiation containing ultraviolet. Schanz, having raised this purple beech under various screens, found that it lost its red anthocyanin color the more the short waves were cut off. He then transplanted one of the plants which had developed large green leaves lacking anthocyanin to the open where it was exposed to the full radiation of daylight. At the end of 14 days all of these green leaves were dead and the new ones that had developed were red in color. Schanz concluded that possibly the red anthocyanin acted as a screen here to protect the plants against ultraviolet radiation. Unfortunately plants that had already developed anthocyanin were not transplanted to the open in a similar manner. Furthermore, other species of plants containing a similar anthocyanin relationship were not injured when placed in the open. This situation might be cleared up if such plants as the purple beech were first grown under conditions in which anthocyanin fails to develop and then exposed to an artificial source of ultraviolet by the same method as was used by Arthur and Newell. Then at least we would be able to ascertain whether such plants were more sensitive to long-wavelength ultraviolet than ordinary plants.

Arthur (7) was able to bring about the development of red pigment in McIntosh apples by irradiating them with a mercury vapor arc in Uviol glass at a distance great enough to prevent injury. Forty hours exposure was necessary to cause this coloration in apples gathered August 25, but the period increased with increase in age of the apple after August 27, and with time of storage. No pigment developed in fruits taken from storage in January. Peelings of apples floating upon water and irradiated developed color similarly, but those killed by heat or alcohol and then irradiated, developed no red color.

A recent note from the New York State Agricultural Experiment Station (4), states that McIntosh apples that had shown no red color originally, became completely red when exposed for 4 or 5 days to a 1500 watt

electric lamp. This would indicate the possibility that other wave-lengths besides ultraviolet may be effective.

While ultraviolet radiation may affect the development of anthocyanin it is definitely known that such radiation is not absolutely necessary for all anthocyanin formation. Popp (106, 107) for instance found that mustard seedlings grown continuously in the dark or grown in the dark and exposed to the mercury arc from which the ultraviolet portion had been eliminated, formed anthocyanin. The fact that beet roots developed in the soil in the absence of all radiation are rich in anthocyanin is well known. That anthocyanin formation is favored by ultraviolet radiation is possibly indicated, however, by experiments such as those just referred to, although ultraviolet effects have never been clearly separated from total radiation intensity or from blue-visible effects.

The effect of ultraviolet radiation upon cell contents

The nature of the influence of ultraviolet rays on the cell contents themselves has been investigated more intensively in the cells of lower plants and animals than in those of higher plants. There is no doubt that the reaction of protoplasm to such irradiation is complex. No attempt will be made in this report to go into the details of such reaction. In general investigations such as those of Downes and Blunt (41, 42), Burge (21, 22), Harris and Hoyt (62), Bovie (18, 19), Barr and Bovie (12), Gates (52, 53, 54), and others have indicated that short wave ultraviolet (below 290 mμ.) causes a cytolysis in lower organisms. Gates found that wave lengths 260 to 270 mμ. produced the maximum bactericidal action, which is contrary to the general findings indicating that the shorter the wave length the greater the bactericidal action. The coagulation of the protoplasm is a prominent factor in this cytolysis. Studies in vitro have demonstrated the coagulation of proteins by ultraviolet radiation. The killing effects of the radiation of an unscreened mercury arc upon the superficial cells of higher plants have been noted by every investigator who has examined such cells, including Maquenne and Demoussy (82), Schroeter (130), Schulze (131), Kluyver (71, 72), Stoklasa (150, 151, 153), Ursprung and Blum (165), Sibilia (145), Delf, Ritson, and Westbrook (37), Martin and Westbrook (86), Nadson and Rochlin (96), Bucholtz (20), and Popp and Brown (109, 110).

Protoplasmic streaming of irradiated cells has been noted in a number of cases. In general the first reaction is a stimulation or increase in the rate of streaming which reaches a maximum, decreases, and finally ceases, the cessation marking the beginning of necrosis of the protoplast. Hertel (64, 65) and Schulze (131) have recorded the retardation and final cessa-

tion of protoplasmic streaming of *Elodea* leaf cells and certain other plant parts under monochromatic radiation of wave-lengths near 275 mμ. and 280 mμ. More recently Noethlin and Rochlin (97) in rather extensive experiments have shown that short wave ultraviolet is more effective than all other regions of the spectrum of a mercury vapor arc in inducing plasma streaming. The elimination of the infra-red by a water screen did not affect the results. They explain Nothmann-Zuckerkandl's (98) failure to observe plasma streaming under the influence of the shorter visible and ultraviolet as due to the fact that the cells were not observed closely after irradiation and that they were killed so rapidly that they showed no great visible differences from living cells when finally observed.

There is evidence that ultraviolet radiation may promote oxidation phenomena. Nadson and Rochlin (95, 96) have thought that this causes among other things the transformation of starch grains into calcium oxalate crystals with sugar probably as an intermediate product. They have illustrated photographically what they thought to be the various visible stages in this transformation. Beauverie and Cornet (13) have thought that ultraviolet radiation produces hydrogen peroxide in the medium which causes a kind of fixation in the structure of the cells of leaves and buds of *Elodea canadensis*. This hypothesis was strengthened by the direct action of hydrogen peroxide used in some experiments. The investigation was to be continued on aerial organs to eliminate the possibility of the intervention of products formed in the medium.

Ultraviolet radiation has been shown to interfere with cell division. Schulze (131) found that the magnesium line at 280 mμ. retarded cell division in *Tradescantia*. Takamine (154) noted the effect of the line 250 mμ. of a mercury arc at distances of ten to twenty centimeters for periods of one half to three hours on the root tips of *Vicia faba*, *Allium cepa*, the pollen mother cells of *Capsella bursa pastoris*, *Lactuca thunbergiana*, and *L. lanceolata platyphylla*. He noted various irregularities including the stricture and breaking up of chromosomes, irregular distribution of chromosomes, and sometimes tripolar divisions of somatic nuclei. In pollen formation not all tetrad cells developed into grains; some disintegrated.

Lepeschkin (78) noted that the rays most active in influencing changes in the permeability of protoplasm were those transmitted through a G586A Corning filter, that is the region 320 to 420 mμ., with a maximum at about 370 mμ.

Short wave ultraviolet in general has been found to weaken or destroy enzyme activity. Green (58) and Hertel (64) reported the weakening of diastase activity, Green using ultraviolet and blue rays, and Hertel monochromatic wave length of 280 mμ. Chauchard and Mazoué (25) and Agul-

hon (5) also report the destruction of enzymes by ultraviolet. Burge, Fischer, and Neill (23) found that pepsin, trypsin, enterokinase, ptyalin, amylopsin, and the proenzyme trypsinogen were all destroyed by ultraviolet radiation. The destruction of enzymes by ultraviolet radiation has led some to believe that ultraviolet kills living cells by destroying the enzymes within them. Burge, however, (21, 22) has demonstrated that ultraviolet may kill bacteria without destroying the intracellular proteolytic enzymes. In these tests he used bacteria which by virtue of the proteolytic enzymes within their cells possess the property of liquifying gelatin. He killed such bacteria by exposure to ultraviolet radiation, ground them up, after centrifuging, with sand and 30 per cent alcohol to extract the enzyme, and found that the treatment had affected the enzymes but slightly since the results of their activity on gelatin were very little different from the results obtained with living bacteria. He concluded that the death of the cells was due to the coagulation of the protoplasm, brought about by the radiation. Fuller (51) reported at the New Orleans meeting of the Botanical Society that catalase and diastase activity were increased in plants exposed to the lethal ultraviolet region. As our only means of detecting enzyme activity is by measuring the end products of its action results may indicate increased action in irradiated plants for several reasons. It may happen that enzymes formerly confined to certain cells are liberated as a result of irradiation and brought into contact with the proper substrate for activity. Maquenne and Demoussy (83, 84, 85) have emphasized that the blackening of leaves is considered as due not to the specific action of ultraviolet rays, but as a result of diastatic or other enzyme activity brought about by the liberation of enzymes formerly confined within certain cells. Evidence in favor of this view was that blackening could be produced by any means which would destroy the protoplasm such as mechanical injury, chloroform, heat, etc. Paine (101) has confirmed the results of Maquenne and Demoussy. Pougnet (112, 113) has called attention to the fact that various odors which are developed from plants under a mercury vapor arc are caused by the splitting of glucosides. This was thought to occur because of changes of permeability of the protoplasts caused by the irradiation which allowed the interaction of enzyme and glucoside, formerly separated from each other. Ultraviolet radiation may also have a direct effect upon the substrates themselves or upon plants without the intervention of any enzyme activity and result in increased quantities of end products which may be similar to those produced by the action of enzymes. Thus Bierry, Henri, and Ranc (15, 16), Euler and Ohlsen (45), and Berthelot and Gaudechon (14) have shown the inversion of saccharose and other sugars by ultraviolet radiation in the absence of enzymes. The whole subject requires further investigation.

Miscellaneous effects of ultraviolet radiation

Studies with ultraviolet radiation have played a prominent part in recent years in vitamin work. Most of the studies, however, have been conducted with animals. In some cases vitamin formation in plants has been attempted by exposing them to ultraviolet radiation, but the ultimate aim of these investigations was to secure vitamins to feed to animals. No attempt will be made in this discussion to review the papers in this field, but the work of Lojkin (79) will serve as an illustration of this type of study. She has made an extensive investigation on certain effects of ultraviolet rays on the vitamin D content of plants as compared with the direct irradiation of the animal. The vitamin D, whether formed in the plant or in the animal, is thought to be due to the activation of ergosterol. Previous experiments by various workers such as Hess and Weinstock, and Steenbock and Black had yielded conflicting results as to the antirachitic properties possessed by various plants. In the experiments of this investigation lettuce, alfalfa, spinach, New Zealand spinach, and soy beans developed a slight potency in solar radiation under a special ultraviolet transmitting glass. Neither these, nor cabbage nor swiss chard produced vitamin D under ordinary glass. Irradiation of plants by a mercury arc gave considerable potency except for cabbage, 30 minute exposures being optimum. Cut plants were more potent than those left attached to the roots during irradiation. The minimum exposure necessary to produce an appreciable amount of vitamin D in plant tissues was found to be considerably longer than that required to impart complete protection by direct irradiation of the animal. Even with filters of comparatively low transmission in the extreme ultraviolet (lower limit 286 mμ.) an irradiation of one minute of the animal gave complete protection. The shorter ultraviolet rays not present in sunlight were said to be of little value in protecting against rickets, probably because of their failure to penetrate into the cells containing the ergosterol. With a sunlight source, 30 minutes per day in winter and 15 minutes in summer protected rats if they were not given a diet which made them grow too fast, under which conditions the more rapid formation of bone tissue made longer exposures necessary. From these experiments it would seem that from a practical standpoint the direct irradiation of the animal was far more efficient than the irradiation of plants later fed to the animal in supplying the animal with a sufficient amount of vitamin D.

The significance to the plant itself of vitamin formation or of the presence of vitamins in plants has not been determined.

A discussion of the relation of ultraviolet radiation to the synthesis of carbohydrates and proteins is beyond the scope of this paper. The reader

is referred to papers such as those of Tolomei (158), Stoklasa (152), Laurent and Marchal (77), and Ursprung (163) for indications of syntheses occurring in plants under ultraviolet radiation or to those of Kniep and Minder (74), Ursprung (164), Warburg (167), Warburg and Negelein (168), and Schmucker (129) for reports on the relative efficiency of various wave lengths for photosynthesis. More references and a discussion of the relation of ultraviolet to photosynthesis can be found in the excellent monographs on photosynthesis by Stiles (149) and by Spoehr (148). A brief summary of this subject may be found in "The Chemistry of Plant Products" by Haas and Hill (61).

Since the time of Sachs (124) and DeCandolle (34) ultraviolet has been said to influence favorably flower formation. Eltinge, Ballan, Westfield College reports, Michigan Station reports, and Tottingham and Moore have all suggested earlier or better flowering in certain cases as an ultraviolet effect, but it has already been noted that such effects were not consistently obtained and were usually associated with temperature or other differences when comparisons were made with control plants. Popp found that elimination of practically all ultraviolet had no effect on the time or amount of flowering of many of his plants. In some cases the earlier flowering plants were those from which practically all ultraviolet was screened off.

That the injurious effects of ultraviolet radiation are only temporary has been emphasized by Sibilia (145), Jacobi (68), Popp and Brown (110) Arthur and Newell (8), and Detwiler (38) who found that temporary effects on general appearance, color, size, general vigor, and weight disappeared when the injurious irradiations ceased, the length of time necessary for this being dependent upon the degree of injury, unless the injury was too severe, in which case the plants died. McCrea (88, 89, 90, 91) found what she thought to be a lasting physiological effect in the greater production of digitalin in *Digitalis purpurea* months after the test plants with the controls had been put outdoors.

The fluorescence of seeds germinating under irradiation by the region 300 to 400 mμ. has been noted by Gentner (56), Mezzadroli and Vareton (94), Foy (47), and Masure (87), but its significance is not known. Gentner has attempted to find out whether the nature of the fluorescence is specific enough that it may be used practically for seed testing, particularly for the differentiation between seed varieties and races. Foy has used this method successfully in diagnosing various types of rye-grass in New Zealand. The annual Italian rye-grass and some or all of the false perennial types exhibit a brilliant blue fluorescence while the true, normal, perennial rye-grass reacts absolutely negatively.

The relation of ultraviolet radiation to transpiration (43), respiration (87), sunscald (80), winter hardening (161), tropisms (46), electric potentials and currents in plants (138) and to various other miscellaneous effects ascribed to it will not be discussed because the evidence is too fragmentary.

CONCLUDING REMARKS

In spite of the many publications on the subject, exact knowledge regarding the influence of ultraviolet radiation upon seed plants other than its destructive action is still to be ascertained. The interest in ultraviolet in recent years has been so widespread as to justify the accusation of some that the subject is a fad. It is to be hoped that the "fad" will not run its course before accurate information has been obtained. Needless to say, such information will not be forthcoming from experiments of short duration, carried out with a few plants under poorly controlled conditions such as have predominated in the work of the past.

Much of the present uncertainty of our knowledge of the effects of radiation upon plants rests upon the complexity of the problem itself. No other environmental factor is so variable or so difficult to control. The fact that plants require visible radiation for normal growth necessitates supplying them with this radiation. Sources of visible radiation usually contain also infra-red radiation. Consequently these factors must be considered and equalized in test cultures and controls when the effects of ultraviolet are to be studied. Total radiation measurements, transmissions of screens, spectrograms of the radiation used, and the like, are in themselves insufficient to give a complete picture of the nature of the radiation reaching plants, although in many papers, even these variables are not given. Few, if any, authors have measured the total energy or the distribution of the energy in the ultraviolet to which results were attributed, to say nothing of the failure to equalize the radiant energy of other wave lengths reaching the test plants as compared with the controls. While it is conceded that these measurements are difficult to make, it must also be admitted that so long as they remain unknown in an experiment the results cannot be attributed to ultraviolet any more than to any other operating variable.

In addition to the necessity of having a complete description of the radiation reaching plants it is no less important to know whether the plants or plant parts studied absorb selectively different portions of the spectrum and to what extent. Possible photochemical reactions in the plant may be greatly accelerated in a relatively narrow region of the spectrum that is strongly absorbed, whereas comparatively high intensities in a region that is feebly or not at all absorbed might be without effect.

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The rate of fall of spores in relation to the epidemiology of black stem rust[1]

HARRY G. UKKELBERG

(WITH FOUR TEXT FIGURES)

INTRODUCTION

The periodic occurrence of epidemics of stem rust in the spring-wheat area has led to investigations of the probable factors involved in their development. Obviously, two of the primary requisites for the development of epidemics are abundant inoculum and some means for its general dissemination. Air currents and high winds are known to play an important rôle in the dissemination of some fungus spores. That they are important also in the dissemination of cereal rusts is generally accepted.

Stakman, Levine, and Wallace (1929) give three possible sources of stem-rust inoculum for the spring wheat area: urediniospores that survive the winter in the North; aeciospores from barberry bushes; and windborne urediniospores from the South. The possibility that cereal rusts that develop in early spring in Mexico and Southern United States serve as inoculum for the northern areas presupposes the long-distance dissemination of spores. Inoculum from the South could migrate in two ways, either by successive northward migration for comparatively short distances or by a continuous journey from the infected areas in the South to the grain fields in the North.

Lambert (1929) discussed the evidence of long-distance dissemination of spores and was of the opinion that under favorable atmospheric conditions stem rust urediniospores could be carried from Texas to the spring-wheat area in three days.

Stakman, Levine, and Wallace (1929) and Wallace (1932) concluded from a comparison of the physiologic forms of stem rust present in the South and the North that very little rust was blown northward in 1926, but that in 1927 and possibly in 1928 a migration of rust occurred. Stakman *et al.* (1923) demonstrated by slide exposures from airplanes that rust spores often reach high altitudes. Urediniospores of *Puccinia graminis* Pers. and *P. triticina* Eriks., as well as spores of other fungi, were found to be fairly common at altitudes up to 10,000 feet.

From these investigations it seems clear that spores may often reach high altitudes and that they probably are carried long distances by favor-

[1] Cooperative investigations by the Division of Barberry Eradication, Bureau of Plant Industry, U. S. Department of Agriculture, and the Agricultural Experiment Station of the University of Minnesota. Paper No. 1135 of the Journal Series of the Minnesota Agricultural Experiment Station.

able winds. Obviously, the rate of spore fall is one factor determining how far they can be carried by the wind. For this reason the studies reported in this paper were made.

The distance spores can be carried by air currents will depend upon three factors: the altitude attained by the spores, their rate of fall in air, and velocity and duration of winds. As spores have a large surface area in proportion to their mass they would fall at a relatively slow rate.

Buller (1909) determined microscopically the rate of fall of basidiospores of some of the Hymenomycetes by means of a specially constructed apparatus consisting of a compressor cell fitted to a horizontal microscope. A small piece of the fruiting body of the fungus was placed in such position that the spores, when liberated, fell vertically across the microscopic field. Fine silk threads were attached to the eyepiece in such manner as to mark off a distance of 4.55 millimeters. The time required for the spores to fall across that part of the microscopic field delimited by the silk thread was determined. It was found that spores of different species fall at different rates, ranging from 0.49 mm. per second in the case of *Collybia dryophila* Fr. to 4.29 mm. per second for *Coprinus plicatilis* Fr. In general, the rate of fall increased directly with the size of the spores, although this was not true in all cases.

McCubbin (1918) determined the rate of fall of air-dried urediniospores of *Cronartium ribicola* Fisher. The spores were released at the top of an 8-ft. cardboard tube and caught on slides placed at the bottom. It was found that urediniospores continued to fall on the slides over a period of 5 minutes. On the first slides exposed after the spores were released, many irregularities were noted, due to the falling of clumps of spores. Spores requiring 5 minutes to fall 8 ft. would fall at the rate of approximately 8 mm. per second.

The rate of fall of urediniospores and aeciospores of *P. graminis* has never been determined. Because of its bearing on the dissemination of cereal rusts by air currents, the rate of fall in still air of spores of four different cereal rusts was studied.

Field observations on the development of rusts indicated that *P. graminis* and *P. triticina* are disseminated over large areas in most years. *P. coronata* Corda, however, although usually abundant in the southern states, seems to migrate northward less frequently. A difference in the rate of fall of spores of different species might account in part for this apparent difference in dissemination.

MATERIALS AND METHODS

The rate of fall of urediniospores was measured in a galvanized-iron cylinder 6 ft. long and 6 in. in diameter (fig. 1). The lower end was closed

and the upper end covered with a tight-fitting lid. Three sides of the cylinder near the lower end were fitted with glass windows 2½ in.×5 in., the lower edge of the windows being 3 in. from the bottom. At the bottom of the cylinder two openings 1 ¼in.×¼ in. were cut on opposite sides, while a hole ¼ in. in diameter was made ¾ in. from the top. A small insect-powder gun was used to discharge the spores into the cylinder through the small hole in the upper end. This method of liberating the spores aided in breaking up spore clusters and resulted in the fall of a maximum number of single spores.

The spores were caught on glass slides covered with a thin film of vaseline and held by a wooden lath approximately 17 in. long and 1⅛ in. wide. Two grooves, slightly larger than the glass slides, cut in the upper side of the lath held the slide in position. This lath was inserted through the openings at the bottom of the cylinder, passing directly through its center and protruding several inches on each side. The lath, when in position, held a slide placed in one of the grooves directly in the center of the tube. A second slide was inserted in the other groove on the outside of the cylinder. After the slide in the tube had been exposed the proper interval, the lath was drawn quickly in one direction to bring the exposed slide to the outside of the cylinder and, at the same time, to carry a fresh slide into the center.

A beam of light from a projection lantern directed through the glass windows made it possible to observe the fall of the spores. By watching the movement of dust particles in the air within the cylinder it was possible to determine the time when convection currents were almost absent

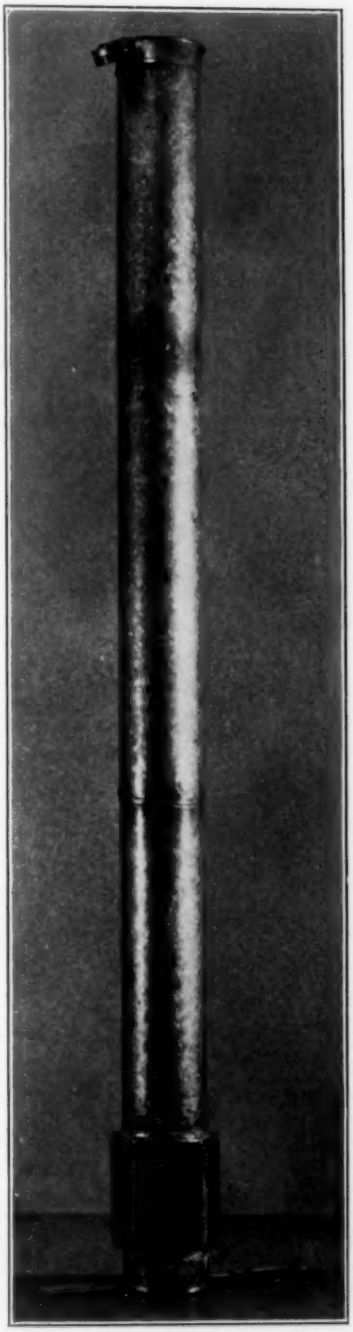

Fig. 1. Galvanized-iron cylinder used in measuring the rate of fall of urediniospores.

and therefore the most suitable time at which to release the spores.

Before each trial the cylinder was carefully washed with water to remove all spores present, after which it was dried over a radiator for a short time and then allowed to cool uniformly to room temperature.

The urediniospores used in the experiment were secured from stock cultures and increased upon suitable seedling plants. Only spores from well-developed pustules were used; they were removed by gently scraping the pustule with a small, rigid spatula. In all cases the spores were air dried for one hour before a test was made. A check slide was exposed for one minute in the cylinder at the beginning of each trial to determine whether the air was free of spores. In no case were any spores caught on check slides.

Slides were changed every 30 seconds from the time the spores were released until no spores were observed falling at the bottom of the cylinder. The entire surface of each slide was examined under low power of a microscope and the number of spores and clumps of spores caught during each 30-second period recorded.

The distance from the point of release at the top of the cylinder to the surface of the slide at the bottom was 180 centimeters; therefore, all spores caught on the slides fell this distance.

The galvanized iron cylinder was found unsatisfactory in measuring the rate of fall of aeciospores because of the difficulty encountered in liberating spores from the aecial cups. Accordingly, a method was devised by which the spores were liberated under more natural conditions.

The special apparatus used (fig. 2) consisted of a glass cylinder approximately 2 ft. long and 1⅞ in. in diameter, a projection lantern to furnish sufficient light, and a microscope mirror to reflect the light upward through the long axis of the cylinder. The bottom of the cylinder was closed by covering with a circular piece of glass somewhat larger than the mouth of the tube and sealed with a mixture of beeswax and paraffin. This bottom could be removed for cleaning simply by melting the paraffin. The cylinder was held in a vertical position by means of a clamp attached to a ring stand. The microscope reflector was fastened directly under and 8 in. below the bottom of the cylinder. At the top of the cylinder was an opening ½ in. in diameter through which the spore material was inserted. This opening was closed with a tight-fitting cork when the trials were being made. To a small glass rod extending through the cork and into the cylinder was fastened a small piece of blotting paper. Freshly cut barberry leaves with well developed aecia of stem rust were attached to this blotting paper, which was moistened at the beginning of each trial.

Under the conditions provided by the above described apparatus the

spores were shot from the aecial cups in large numbers. The reflector below the cylinder was tilted at an angle, and when light from the projection lantern was focused on it a beam was thrown upward through the full length of the cylinder. In this beam of light the falling spores could easily be observed. In order to eliminate the possibility of air currents being set up in the cylinder by heat from the projection lantern, a water bath was

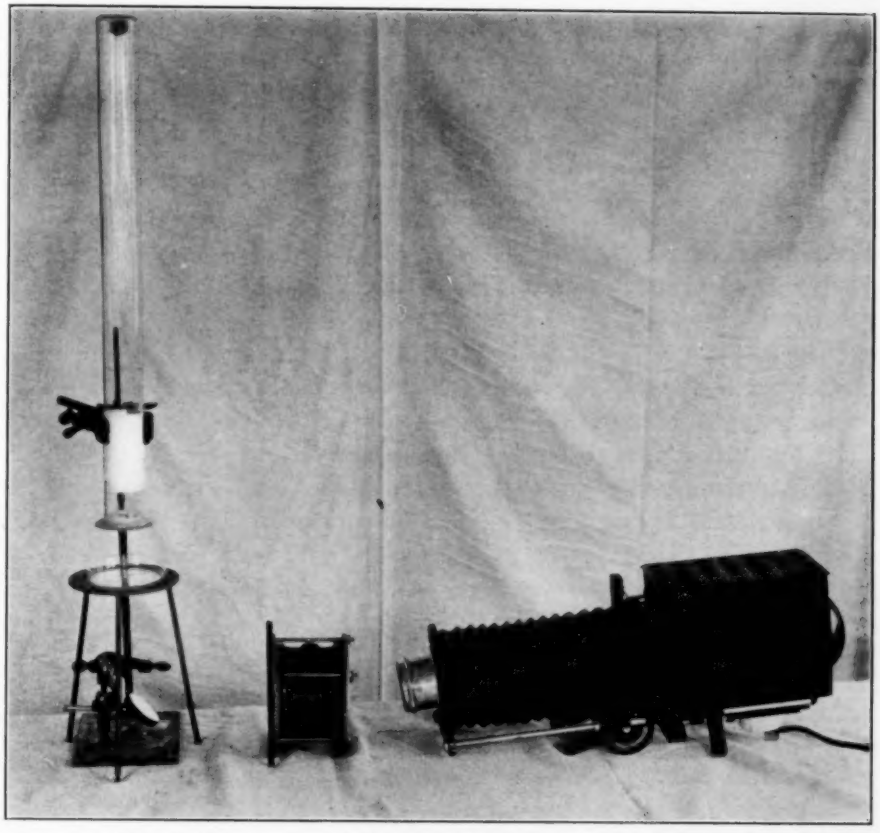

Fig. 2. Apparatus used in measuring rate of fall of aeciospores.

placed between the projection lantern and the reflector. A Petri dish filled with water and placed between the reflector and the bottom of the cylinder provided further for the elimination of heat.

A distance of 30 cm. was measured off on the cylinder and marked with a wax pencil, the upper mark being 3 in. below the infected leaves. The time required for the aeciospores to fall the distance between the marks on the cylinder was observed and recorded by a stop watch. The procedure was as follows: An infected barberry leaf was fastened to the blotting pa-

per, which, after being moistened, was inserted into the upright cylinder, with aecia facing downward. In a short time ejection of aeciospores began and they slowly fell to the bottom of the cylinder, their course being easily followed in the beam of light. Single spores were selected at random and their passage between the 30-cm. marks on the cylinder timed with the stop watch and recorded to the nearest second. Often large numbers of aeciospores were ejected almost simultaneously and fell at a uniform rate more or less as a cloud. One spore from such a group was traced in its fall through the cylinder. After a little experience, no difficulty was encountered in following with the eye the fall of each spore selected.

RATE OF FALL OF UREDINIOSPORES

The rate of fall of urediniospores of *Puccinia graminis tritici* Eriks. and Henn., *P. graminis secalis* Eriks. and Henn., *P. coronata avenae* (Cda.) Eriks. and Henn., and *P. triticina* was determined. Ten separate trials were made with spores of *P. graminis tritici*, while five tests were made with the other rusts.

The first spores to fall the length of the cylinder were in clusters, each cluster containing various numbers of spores. All having more than five spores were placed in one class because of the difficulty of determining the exact number, while clusters with five spores or fewer were classified according to the number of spores in each. Table 1 shows the total number of single spores and the number and magnitude of spore clusters of *P.*

TABLE 1

Number of individual urediniospores and spore clusters of Puccinia graminis tritici deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

MAGNITUDE OF SPORE CLUSTER	EXPOSURE PERIODS (NO. OF SECONDS AFTER SPORES WERE LIBERATED)												
	0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240	240–270	270–300	330–330	300–360	TOTAL
	NUMBER OF SINGLE UREDINIOSPORES AND SPORE CLUSTERS DEPOSITED ON SLIDE												
Individual spores	0	0	34	1004	1669	1234	588	340	144	74	27	8	5122
Clusters of 2 spores	0	3	74	230	146	39	2	0	0	0	0	0	494
Clusters of 3 spores	0	3	70	65	21	4	0	0	0	0	0	0	163
Clusters of 4 spores	0	2	51	18	5	0	0	0	0	0	0	0	76
Clusters of 5 spores	0	2	19	5	0	0	0	0	0	0	0	0	26
Clusters of more than 5 spores	1	67	70	8	0	0	0	0	0	0	0	0	146

graminis tritici deposited on slides during the various periods of exposure. Clusters of spores fell with greater velocity than individual spores and, as the number of spores in a cluster increased, their average rate of fall also increased. Of the large clusters having more than five spores each, 94.5 per cent reached the slides 1½ minutes after they were liberated (Table 2), while in that time only 0.7 per cent of the single spores were caught.

TABLE 2

Percentage of individual urediniospores and spore clusters of Puccinia graminis tritici deposited 180 cm from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

MAGNITUDE OF SPORE CLUSTER	EXPOSURE PERIODS (NO. OF SECONDS AFTER SPORES WERE LIBERATED)												
	0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240	240–270	270–300	300–330	330–360	TOTAL
	PERCENTAGE OF SINGLE UREDINIOSPORES AND SPORE CLUSTERS DEPOSITED ON SLIDE												
Individual spores	0	0	7.0	19.6	32.6	24.1	11.5	6.6	2.8	1.4	0.5	0.2	100
Clusters of 2 spores	0	0.6	15.0	46.6	29.5	7.9	0.4	0	0	0	0	0	100
Clusters of 3 spores	0	1.8	42.9	39.9	12.9	2.5	0	0	0	0	0	0	100
Clusters of 4 spores	0	2.6	67.1	23.7	6.6	0	0	0	0	0	0	0	100
Clusters of 5 spores	0	7.7	73.1	19.2	0	0	0	0	0	0	0	0	100
Clusters of more than 5 spores	0.7	45.9	47.9	5.5	0	0	0	0	0	0	0	0	100

The rate of fall of spore clusters is of minor importance from the standpoint of wind dissemination. Although spores may leave pustules in groups, they probably soon become separated under natural conditions. It is only the spores that reach high altitudes that would be important from the standpoint of long-distance dissemination, and, according to the results of slide exposures, individual spores are most likely to be carried to great heights. Although spores caught on slides exposed from airplanes have been found occasionally in groups of two or three, the majority caught at high altitudes have been individual spores.

Great variation was found in the time required for single urediniospores to fall the length of the cylinder. This was true in the case of all rusts with which tests were made. Some variation occurred in the different trials, due probably to slightly different conditions at the time of each test. Although no trials were made when air currents were noticeably present in the cylinder, it is quite possible they were not eliminated entirely and affected to a slight extent the rate of fall. The number of trials made, however, probably overcame the irregularity of any one trial.

A few spores of *P. graminis tritici* fell 180 cm. in 1½ minutes, while other spores required 6 minutes to fall that distance. The largest deposit of spores on any slide occurred during the period from 2 to 2½ minutes after liberation. This was true also in the case of *P. graminis secalis* and *P. triticina*, while the largest deposit of spores of *P. coronata* occurred during the next period, or from 2½ to 3 minutes after liberation. Summaries of the totals obtained for the four rusts during each exposure period are given on a numerical basis in table 3, on a percentage basis in table 4, and shown graphically in figure 1.

TABLE 3

Number of uredinios pores of four different cereal rusts deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

RUSTS	EXPOSURE PERIODS (NO. SECONDS AFTER SPORES WERE LIBERATED)														TOTAL
	0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240	240–270	270–300	300–330	330–360	360–390	390–420	
	NUMBER OF UREDINIOSPORES DEPOSITED ON SLIDES														
Puccinia graminis tritici	0	0	34	1004	1669	1234	588	340	144	74	27	8	0	0	5122
P. graminis secalis	1	3	88	424	637	522	419	245	134	112	54	27	4	0	2670
P. coronata	0	0	22	190	805	1317	977	355	166	108	71	35	10	6	4062
P. triticina	0	0	44	490	517	169	97	77	37	19	13	5	0	0	1468

TABLE 4

Percentage of uredinios pores of four different cereal rusts deposited 180 cm. from point of liberation on glass slides exposed successively for 30-second periods in a closed cylinder

RUSTS	EXPOSURE PERIODS (NO. SECONDS AFTER SPORES WERE LIBERATED)														TOTAL
	0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–240	240–270	270–300	300–330	330–360	360–390	390–420	
	PERCENTAGE OF UREDINIOSPORES DEPOSITED ON SLIDES														
Puccinia graminis tritici	0	0	0.7	19.6	32.6	24.1	11.5	6.6	2.8	1.4	0.5	0.2	0	0	100
P. graminis secalis	+	0.1	3.3	15.9	23.9	19.5	15.7	9.2	5.0	4.2	2.0	1.0	0.2	0	100
P. coronata	0	0	0.5	4.7	19.8	32.4	24.1	8.7	4.1	2.7	1.8	0.9	0.2	0.1	100
P. triticina	0	0	3.0	33.4	35.2	11.5	6.6	5.2	2.5	1.3	1.0	0.3	0	0	100

A comparison of results with the different rusts indicates some difference in the rate of fall. The largest percentages of spores of *P. triticina* (table 4) were deposited on the slides during the 90–120 and 120–150 second periods. In the case of *P. graminis* the heaviest deposits occurred during the 120–150 and 150–180 second periods, while for *P. coronata* the heavy spore deposits were made in the periods from 150 to 180 seconds and from 180 to 210 seconds. A larger percentage of spores of *P. triticina*, there-

fore, fall more rapidly than those of other rusts. Two and one-half minutes after liberation, 71.6 per cent of the spores of this rust had fallen the length of the cylinder, 52.9 per cent of the spores of *P. graminis tritici*, 43.2 per cent of those of *P. graminis secalis*, and only 25.0 per cent of *P. coronata* spores.

The greatest variation in rate of fall was found in spores of *P. graminis secalis*. It is quite probable, however, that the four spores of this rust caught during the first minute after liberation fell part of the distance in a cluster, thus explaining how they could traverse the distance in so short a time. However, the cohesiveness of urediniospores appears to be great, and it is doubtful if, in many cases, single spores were separated from groups during their drop in the cylinder.

The average number of seconds required for the single spores of the four different rusts to fall 180 cm. and the average rate of fall are shown in table 5. The means were calculated from the formula $\sum fx/N$ when f = the frequency in a class (number of spores deposited on each slide during each 30-second period in this case), x = the class center, and N = the total number of spores.

TABLE 5

Average rate of fall in still air of urediniospores of four cereal rusts

CEREAL RUSTS	AVERAGE NO. SECONDS REQUIRED TO FALL 180 CM.	AVERAGE RATE OF FALL (MM. PER SECOND)	CALCULATED TIME REQUIRED TO FALL 1,000 FT.
Puccinia graminis tritici	155.63±0.41	11.57±0.03	7 hrs., 19 min.
P. graminis secalis	170.09±0.76	10.58±0.05	8 hrs.
P. coronata	180.13±0.50	10.00±0.03	8 hrs., 28 min.
P. triticina	142.60±0.83	12.62±0.07	6 hrs., 43 min.

As each slide was exposed for 30 seconds, it was necessary in calculating the means and probable errors to use a class center. The mean of each exposure period was used; for example, all spores deposited on the slide exposed during the period from 60 to 90 seconds after liberation were considered to have fallen 180 cm. in 75 seconds, while for those caught during the period 90–120 seconds, 105 seconds was taken as the class average. With this method the assumption is made that the spores were deposited on the slides uniformly throughout each exposure period, although this probably did not occur. The slight error thus introduced would have very little effect on the means, as the variations would be in both directions. The probable errors of the means were calculated from the formula $\text{P. E.} = \frac{.6745\sqrt{\frac{\sum fx^2}{N} - \bar{x}^2}}{\sqrt{N}}$ where x = the class center, f the class frequency,

$\bar{x}^2$ = the mean, and N = the total number of spores. From table 5 it is seen that the urediniospores of *P. triticina* fall more rapidly than those of the other three rusts, while *P. coronata* has the slowest average rate of fall.

The average velocity of fall of urediniospores of *P. graminis tritici* was found to be approximately 11.5 mm. per second, or a millimeter per second less than that of *P. triticina*, and 1 mm. more than the spores of *P. graminis secalis*. But the variation among spores of the same rusts was much greater than the variation between spores of the different rusts. In comparing the difference between the means (table 6), it is found that they exceed their

TABLE 6

Summary of differences between the means of the rate of fall of urediniospores of four cereal rusts in still air in a closed cylinder

RUSTS COMPARED	DIFFERENCE IN MEANS (MM. PER SECOND)	DIFFERENCE DIVIDED BY P.E.
Puccinia graminis tritici and *P. triticina*	1.05±0.076	13.82
P. graminis tritici and *P. graminis secalis*	0.99±0.058	17.07
P. graminis tritici and *P. coronata*	1.57±0.042	37.38
P. triticina and *P. graminis secalis*	2.04±0.086	23.72
P. triticina and *P. coronata*	2.62±0.076	34.47
P. graminis secalis and *P. coronata*	0.58±0.058	10.00

probable errors 10 times or more and are therefore undoubtedly statistically significant. The chances are infinitesimally small that these differences are due to errors of random sampling. It may be concluded, therefore, that there is a significant difference in the rate of fall of urediniospores of the four rusts studied under the conditions of the experiment. The urediniospores of *P. triticina* fall most rapidly, those of *P. graminis tritici* somewhat more slowly than those of *P. triticina*, but more rapidly than those of *P. graminis secalis* and *P. coronata*, while spores of *P. graminis secalis* fall slightly more rapidly than those of *P. coronata*, which have the slowest rate of fall.

Special mention may be made of the difference between the rate of fall of spores of *P. graminis tritici* and that of spores of *P. graminis secalis*, physiologic varieties of the same species of rust. The difference of 0.99 mm. per second is 17.07 times its probable error and therefore can not be attributed to random sampling. Levine (1923) found a significant difference in size of urediniospores of these two rusts when grown under uniform conditions. The spores of *P. graminis tritici* averaged 5.26μ longer and 2.60μ wider than those of *P. graminis secalis*. This might easily account for the difference in rate of fall, as the velocity of fall of the larger spores would be greater, assuming the density to be the same.

The foregoing results are interesting when considered from the standpoint of wind dissemination of urediniospores. Table 5 gives the time required for the average spore of the various rusts studied to fall 1,000 ft. in still air, based upon their rate of fall as determined under the conditions of the experiment. In the case of *P. graminis tritici*, over seven hours would be required for urediniospores to reach the ground from this elevation, provided no air currents influenced the fall. As spores are known to be numerous at much higher elevations, it is apparent that urediniospores of rusts as well as spores of other fungi can be carried long distances by strong winds, unless precipitated by rain or dew or influenced by convection currents.

RATE OF FALL OF AECIOSPORES

The common barberry has long been known to be a source of inoculum of black stem rust of grain and grasses. Many observations have been made on the development of local epidemics of stem rust near barberry bushes. Christensen[2] described the development of a local epidemic in 1922 near Northfield, Minn., where primary infection was traced for a distance of two miles from a group of infected barberry bushes.

No direct evidence of long-distance dissemination of aeciospores has been presented, but it seems probable that they may be carried considerable distances by air currents. Stakman et al. (1923) caught aeciospores on vaseline-covered slides exposed over infected barberry bushes at altitudes ranging from 100 to 7,000 ft. This indicates that aeciospores are carried upward to high altitudes, as well as urediniospores. It appears, therefore, that under favorable meteorological conditions they could be transported long distances and thereby serve as inoculum for areas at considerable distances from the infected bushes.

The rate of fall of aeciospores may be important when considering their long-distance dissemination by winds. Accordingly, the rate of fall of aeciospores of *Puccinia graminis tritici* and *P. graminis secalis* was determined by the method already described. The time required for 700 spores of each variety of rust to fall 30 cm. was recorded.

That some aeciospores were being liberated in clusters of several spores was soon evident after watching the fall of the spores in the glass cylinder. Particles of larger size and falling at a more rapid rate than the majority were observed. Especially was this true at the beginning of the discharge of spores from a particular spore horn. Often pieces of the spore horn would break off and fall to the bottom of the cylinder. In order to determine what these more rapidly falling particles were, the bottom of the cylinder was

[2] From unpublished observations made by Dr. J. J. Christensen.

removed and some of them caught on vaseline-covered glass slides. Examination of these slides under the microscope showed that some of the aeciospores were in short chains and clusters of varying numbers. By far the greatest number of particles, however, were single aeciospores.

Particles of apparently larger size and falling faster than the majority were disregarded and the rate of fall of only what appeared to be single spores recorded. This was not difficult, however, as often hundreds of spores falling more or less uniformly could be seen in the cylinder at one time. That a variation existed in the rate of fall of single spores was evident after watching the process for a time. Spores that appeared to fall approximately at the same rate would gradually become separated because of a difference in their rate of fall. On the other hand, it was observed that

TABLE 7

Number of aeciospores of two varieties of Puccinia graminis that fell 30 centimeters, in a glass cylinder, in different lengths of time, and their average velocity

TIME (IN SECONDS)	NUMBER OF SPORES	
	TRITICI	SECALIS
20	2	—
21	4	—
22	10	5
23	19	31
24	40	37
25	62	50
26	95	57
27	83	64
28	73	81
29	62	87
30	60	80
31	49	48
32	45	34
33	39	22
34	20	15
35	20	14
36	12	13
37	5	13
38	—	11
39	—	10
40	—	9
41	—	7
42	—	6
43	—	4
44	—	2
Average time	28.4 ± 0.09	29.4 ± 0.11
Average velocity (in mm. per second)	10.56 ± 0.03	10.20 ± 0.04

several spores would sometimes maintain their same positions relative to each other all the way down the cylinder.

All the data on rate of fall were obtained in a basement room in which the temperature was relatively constant. Convection currents within the cylinder could, of course, influence the rate of fall of the spores, but in practically all cases the spores fell in a direct line without noticeably changing their rate or direction of fall. Care was always exercised not to touch the cylinder during the trials. If, as in a few cases, convection currents

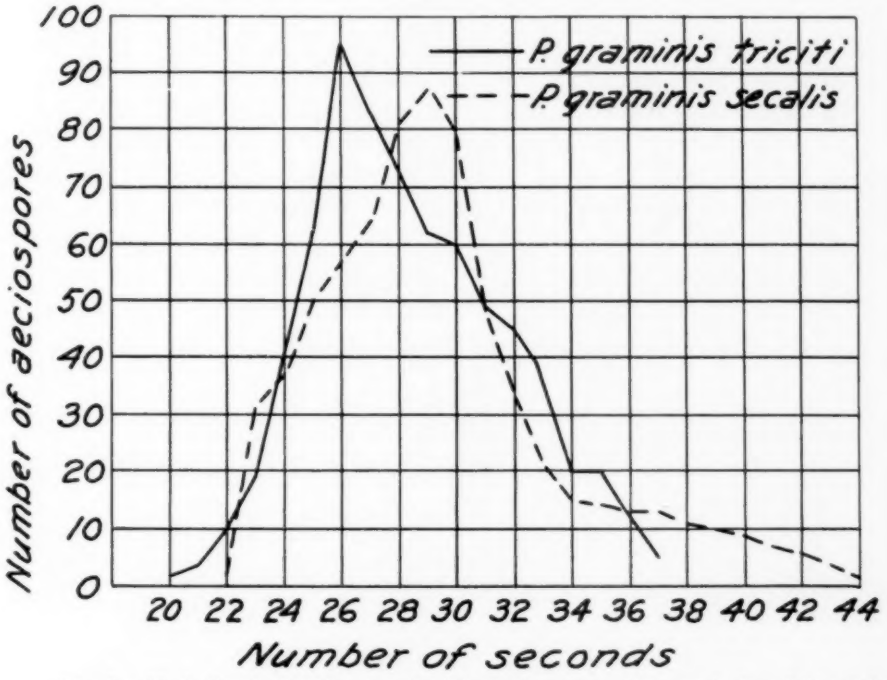

Fig. 3.—Variation in the time required for aeciospores of two varieties of *Puccinia graminis* to fall 30 centimeters in a glass cylinder.

seemed to be influencing the path of the spores, no measurements were recorded.

The action of convection currents could easily be demonstrated by placing the hand at the bottom of the cylinder. When this was done, the body heat soon set up convection currents inside the cylinder, which would not only influence the rate of fall of spores but would actually carry spores upward from the bottom to the top of the cylinder. Because of the fact that these induced convection currents could easily be observed, it is thought that if currents strong enough to influence the rate of fall had been present when measurements were made, they also would have been observed.

There was considerable variation in the rate of fall of aeciospores under the conditions of the experiment, as shown in table 7 and graphically in figure 2. The range in the time required to fall 30 cm. was from 20 to 37 seconds in the case of *P. graminis tritici* and from 22 to 44 seconds for *P. graminis secalis*. Aeciospores of *P. graminis tritici* fell at an average rate of 10.56 ± 0.03 mm. per second, and those of *P. graminis secalis* at 10.20 ± 0.04 mm., the difference being 0.36 ± 0.05 mm. per second. This difference

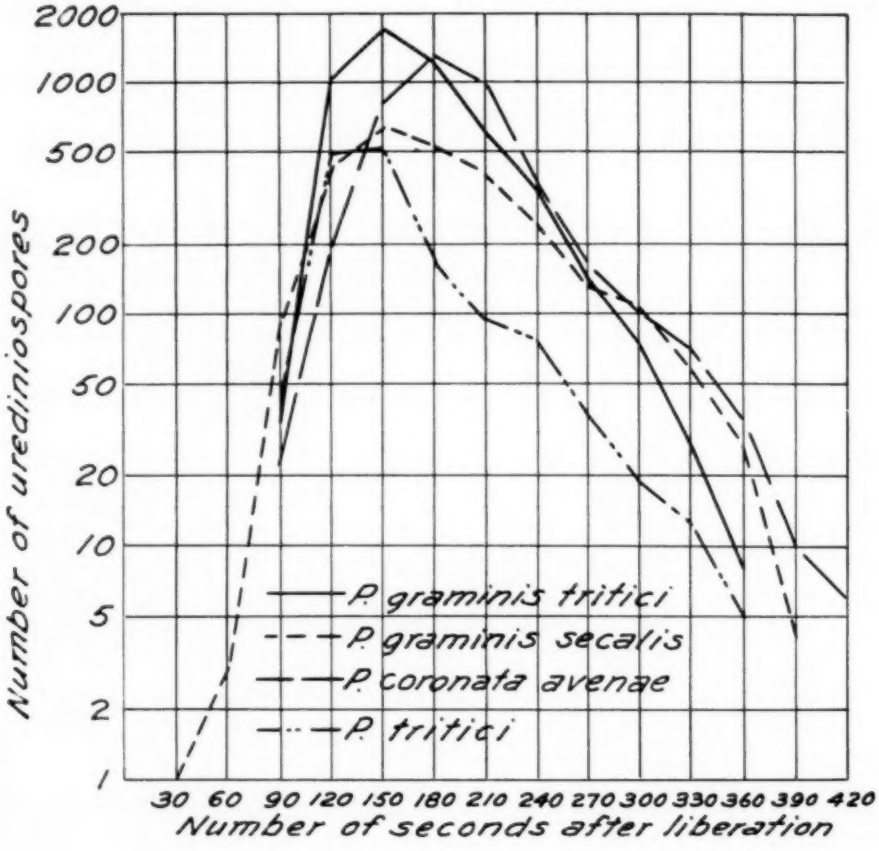

Fig. 4.

is more than seven times its probable error and therefore statistically significant, the chances being more than 400,000 to 1 that it was not due to random sampling. This difference in rate of fall may be due to difference in spore size, as in the case of urediniospores. Levine (3) found that aeciospores of *P. graminis tritici* averaged 2.62μ longer and 2.20μ wider than those of *P. graminis secalis*.

It is interesting to note that urediniospores of *P. graminis tritici* also

have a higher rate of fall and are somewhat larger than urediniospores of *P. graminis secalis*. When comparing the rate of fall of urediniospores and aeciospores, it is found that urediniospores of *P. graminis tritici* fall approximately 1 mm. per second faster than aeciospores, while the urediniospores of *P. graminis secalis* fall 0.38 mm. per second faster than the aeciospores. In both cases the urediniospores are larger than aeciospores.

The size of spores can not be considered the only factor responsible for the differences in the rate of fall. Density and shape might also be important, but the size of spores would influence the rate of fall if the other two variables were constant.

As aeciospores fall more slowly than urediniospores in still air, their dispersal distance would theoretically be greater than that of urediniospores under similar meteorological conditions. The rate of fall of aeciospores indicates that they could easily be carried to high altitudes by convection currents, as well as long distances by favorable winds.

In order to test the accuracy of the two methods used in measuring the rate of fall of spores, the rate of fall of urediniospores of *P. graminis tritici* was measured by the method used in determining that of aeciospores.

A leaf of Little Club wheat, heavily infected with the uredinial stage of

TABLE 8

Number of urediniospores of Puccinia graminis tritici that fell 30 centimeters, in a glass cylinder, in different lengths of time, and their average velocity

TIME (IN SECONDS)	NUMBER OF SPORES
18	3
19	5
20	11
21	23
22	31
23	44
24	57
25	57
26	63
27	48
28	38
29	36
30	26
31	20
32	13
33	13
34	9
35	3
Average time	20.07 ± 0.11
Average velocity (in mm. per second)	11.51 ± 0.05

P. graminis tritici, was fastened to the glass rod used to hold the infected barberry leaves. By gently tapping this rod, urediniospores were induced to fall to the bottom of the cylinder. It was then possible to measure their rate of fall by the method used for aeciospores. The time required for 500 urediniospores to fall 30 cm. was determined in this manner. Results are given in table 8. It will be seen that the average rate of fall for 500 urediniospores was 11.51 ± 0.05 mm. per second as determined by this method. The rate of fall for urediniospores of *P. graminis tritici*, determined by using the galvanized cylinder, was 11.57 ± 0.03, the difference between the two methods being 0.06 ± 0.06 mm. per second. This difference is only as great as its probable error and, therefore, probably due to chance.

The two methods used were quite different but gave practically the same results. This would indicate that both methods were accurate.

DISCUSSION AND CONCLUSIONS

The theoretical dispersal distance of a rust spore would be determined by its rate of fall, altitude attained, and wind velocity. Assuming that an average urediniospore of *P. graminis tritici* had reached an altitude of 5,000 ft., it would require 36 hours and 35 minutes to reach the ground. If it were being carried by a 30-mile wind its dispersal distance would be approximately 1100 miles. With the great variation that exists in rate of fall of spores of any one rust, the theoretical dispersal distance would also vary. About 45 per cent of the urediniospores of *P. graminis tritici* fall more slowly than the average, and their dispersal distance would accordingly be increased. Although differences exist in the average rates of fall of urediniospores of the four rusts studied, they are of minor importance when considered from the standpoint of long-distance dissemination. The spores of all rusts fall so slowly that after having reached a high altitude they would be carried long distances under favorable conditions. In the hypothetical case outlined above, urediniospores of *P. graminis tritici* were shown to have a dispersal distance of approximately 1100 miles. Under the same conditions, *P. triticina* would have a theoretical dispersal distance of approximately 1,000 miles, *P. graminis secalis* 1,200 miles, and *P. coronata* 1,270 miles. With the variation that exists within each rust, a few spores of each would be carried approximately the same distance. The greatest difference would be in the percentage of spores of each rust carried different distances. A larger percentage of urediniospores of *P. coronata avenae* would be carried a given distance than spores of the other rusts studied.

In nature, air currents no doubt are important factors in the time required for a spore to reach the ground from a given altitude. The fact that

spores reach elevations of 10,000 ft. indicate that they are rather easily carried upward against the force of gravity. With the currents and cross currents that exist in nature, the paths of spores being carried long distances can only be conjectured. A spore transported at the rate of one mile an hour would travel at the speed of 447 mm. per second. This is 39 times as fast as the average spore of *P. graminis tritici* falls in still air. According to the *Official Record*[3] for November 20, 1930, a wind blowing at less than one mile an hour allows smoke to rise vertically and therefore would not be perceptible. A convection current traveling upward from the ground at the rate of 1/38 mile an hour or more would carry spores upward as long as these currents continued. Currents at that speed would not allow spores to drop. Convection currents no doubt travel downward as well as away from the earth's surface at various times and would carry with them spores from the upper air. The combined effect of gravity and convection currents would greatly increase the rate of fall of spores; therefore under certain atmospheric conditions the dispersal distance would be greatly reduced.

That urediniospores of stem rust which develop early in Mexico and Texas could be transported in a few days to the spring wheat area of the United States is at least theoretically possible. It also seems reasonable to suppose that sometime during the growing season conditions are favorable for such transportation to take place. The rate of fall of aeciospores also indicates that they too may be carried long distances and that therefore the common barberry may serve as a source of stem-rust inoculum for fields at considerable distances from infected bushes.

SUMMARY

1. Clusters of urediniospores fall at a higher average rate of speed in still air than single urediniospores.

2. The average rate of fall of clusters of spores increases as the number of spores in a cluster increases.

3. The average rate of fall in still air of urediniospores of *Puccinia graminis tritici* was found to be 11.57 ± 0.03 mm. per second, for *P. graminis secalis* 10.58 ± 0.05, for *P. coronata avenae* 10.00 ± 0.03, and for *P. triticina* 12.62 ± 0.07 mm. per second.

4. The observed difference in the rate of fall of urediniospores of the four cereal rusts was found to be statistically significant.

5. The velocity of fall of aeciospores of *P. graminis tritici* and *P. graminis secalis* was found to be less than that of urediniospores of these rusts.

[3] The Official Record. U. S. Department of Agriculture.

6. The rate of fall of aeciospores of *P. graminis tritici* and *P. graminis secalis* in still air was 10.56 ± 0.03 and 10.20 ± 0.04 mm. per second respectively.

7. The observed difference in rate of fall of aeciospores of the two varieties of rust was found to be statistically significant.

8. The average theoretical dispersal distance of urediniospores that have reached an altitude of 5,000 feet and are being carried by a 30-mile wind ranged from 1,000 miles for *P. triticina* to 1,270 miles for *P. coronata*. Under the same conditions *P. graminis tritici* would have an average dispersal distance of 1,100 miles and P. graminis secalis 1,200 miles.

9. The average theoretical dispersal distance of aeciospores, based on their rate of fall, is greater than that of urediniospores.

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INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1932

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